

# SNAKES OF THE GENUS *LIOPHOLIDOPHIS* (COLUBRIDAE) FROM EASTERN MADAGASCAR: NEW SPECIES, REVISIONARY NOTES, AND AN ESTIMATE OF PHYLOGENY

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Notes on MNHN 1988-331 (Genus and Species

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**ABSTRACT.** Two new species of the Madagascan snake genus *Liopholidophis* are described, and the genus is partially revised to clarify the status of species occurring in the Ranomafana National Park (RNP), eastern Madagascar. Nine species of *Liopholidophis* are recognized herein; with the exceptions of *L. pinguis* Parker and *L. stumpffi* (Boettger), all are known from the RNP. These are *rhadinaea*, new species, *epistibes*, new species, *dolicocercus* (Peracca), *grandidieri* Mocquard, *infrasignatus* (Günther), *lateralis* (Duméril, Bibron, and Duméril), *pinguis* Parker, *sexlineatus* (Günther), and *stumpffi* (Boettger). *Dromicus doliocercus* Peracca is here resurrected from the synonymy of *L. sexlineatus*. *Ptyas infrasignatus* Günther is resurrected from the synonymy of *lateralis* and recognized as a senior synonym of *Liopholidophis thieli* Domergue of recent authors. *Liopholidophis stumpffi* (Boettger) (type locality, Nosy-Be) appears to be restricted to northern Madagascar, at least the island of Nosy-Be and the vicinity of Montagne d'Ambre. But the name *stumpffi* has recently been misapplied to a wide-ranging species of the eastern rainforests that is also known from northern Madagascar in the vicinities of Mahajanga and Montagne d'Ambre. This previously unnamed species is the one described herein as *L. epistibes*, new species. *Liopholidophis rhadinaea*, new species, is known from the RNP and from near the Perinet (Andasibe) reserve.

A key to the species is presented. Two species groups earlier recognized by Parker (1925)—the *sexlineatus* group and the *stumpffi* group—are retained, and evidence supporting the monophyly of each is summarized. The *sexlineatus* group includes the species *sexlineatus*, *dolicocercus*, *grandidieri*, *pinguis*, and *rhadinaea*, new species. The *stumpffi* group includes *stumpffi*, *lateralis*, *infrasignatus*, and *epistibes*, new species. Hemipenes of all species are bilobed, non-capitate, and acalculcate (entirely spinose), with deeply bifurcate centrolineal sulci spermatici. Otherwise, details of hemipenial morphology differ substantially between the species groups. Peculiar apical structures are present in *dolicocercus*, *rhadinaea*, and *sexlineatus*, but hemipenes of the *sexlineatus* group in general are rather dissimilar. Hemipenes of species

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in the *stumpffi* group are all characterized by an unusual "umbelliform" depression at the tips of the lobes.

The *sexlineatus* group is characterized (among other features) by two characters that are highly unusual for colubrids: (1) extraordinary sexual dimorphism in tail length (except in the plesiomorphic species, *pinguis*, in which the dimorphism is reduced, tails of males average >40% of total length [ $\geq 13\%$  difference between means of proportional tail length of the two sexes]), and (2) male superiority in body size and ventral counts. The first character is unknown in snakes outside the *L. sexlineatus* group. In contrast, the *stumpffi* group lacks these unusual features. A phylogenetic hypothesis supported by characters of external morphology, hemipenes, skulls, and behavior suggests the following relationships: ((((*dolicocercus*, *grandidieri*), *rhadinaea* new species), *sexlineatus*), *pinguis*); and ((*stumpffi*, *epistibes* new species), *infrasinatus*, *lateralis*).

Although the species groups of *Liopholidophis* appear to be monophyletic, no strong evidence supports the monophyly of *Liopholidophis sensu lato*. However, revision of the generic concept is not warranted until broader relationships among Malagasy colubrids are better understood. Problems concerning the generic status are highlighted by similarities among *Liopholidophis rhadinaea*, new species, several species in the genus *Liophidium*, and a specimen resembling *L. rhadinaea*, new species, in external and hemipenial characters, but whose generic and species placement is enigmatic.

Species of *Liopholidophis* are diurnal and terrestrial, except for *sexlineatus*, which is semiaquatic (no observations for *pinguis* and *stumpffi*). Species of *Liopholidophis* consume primarily frogs (one chameleon record; no data for *pinguis*, *grandidieri*, and *stumpffi*). Most dietary items for *infrasinatus*, *epistibes*, new species, and *dolicocercus* were terrestrial microhylid frogs (*Plethodontohyla* spp.); two records for *rhadinaea*, new species, were clutches of frog eggs; *sexlineatus* consumed *Heterixalus* (Hyperoliidae) and *Ptychadena* (Ranidae); *lateralis* consumed *Mantidactylus* and *Ptychadena* (Ranidae), and *Boophis* (Rhacophoridae). Species of *Liopholidophis* are probably oviparous with the exception of *sexlineatus*, which appears to be viviparous (data somewhat equivocal for *dolicocercus*; no data for *stumpffi* and *pinguis*).

## INTRODUCTION

The Madagascan snake genus *Liopholidophis* (Colubridae) as presently defined (Mocquard, 1904; Guibé, 1958) includes rather generalized terrestrial to semi-aquatic snakes. Several nominal species, including *grandidieri* Mocquard, *dolicocercus* Peracca, *sexlineatus* Günther, and a new species described herein, exhibit the

unusual characteristic of considerable sexual dimorphism in tail length, a character used by Mocquard (1904) in defining the genus. In these species the tail of males averages >40% of total length, whereas in females the tail is usually <30% of total length (>50% and 35% for males and females, respectively, in *grandidieri*) (see additional comments herein). In other colubrids, including other species of *Liopholidophis*, the tails of males and females do not show such exaggerated differences in length, and the sexes overlap in the relative proportion of tail to total length. The monophyly of *Liopholidophis sensu lato* has never been explicitly justified and will be considered in detail later in this paper.

Most nominal taxa of *Liopholidophis* were described in the first half-decade of the twentieth century or earlier. Their nomenclatural history is summarized in the species accounts. Present understanding of *Liopholidophis* stems primarily from the generic summaries of Parker (1925), Guibé (1954, 1958), and Domergue (1969, 1973). Parker (1925) described a new species (*pinguis*) and informally recognized two species groups within *Liopholidophis*: a "sexlineatus group" including *grandidieri*, *dolicocercus*, and *sexlineatus*, based on the shared characters of extreme sexual dimorphism in tail length and 17 midbody scale rows; and a "stumpffi group," including *lateralis* and *stumpffi*, which lack the extreme tail dimorphism and have 19 midbody scale rows. Parker left *pinguis*, which shares 17 midbody scale rows with the *sexlineatus* group but has reduced sexual dimorphism in tail length, unplaced in either group. Subsequently, Guibé (1958) synonymized *dolicocercus* with *sexlineatus*, and *stumpffi* was first synonymized with *lateralis* (Guibé, 1954), and then resurrected (Domergue, 1973). Domergue (1973) described a new species, *thieli*, and also (Domergue, 1969) recognized that *L. pseudolateralis* Guibé (1954) was a synonym of *Dromicodryas bernieri* (Duméril, Bibron, and Duméril, 1854). These changes have resulted in the presently recognized species of *Liopholidophis*: *grandidieri*

Mocquard (1904), *sexlineatus* (Günther, 1882), *pinguis* Parker (1925), *lateralis* (Duméril, Bibron, and Duméril, 1854),<sup>2</sup> *stumpffi* (Boettger, 1881a,b), and *thieli* Domergue (1973) (e.g., Glaw and Vences, 1994). At least one undescribed species from northern Madagascar is known (Raxworthy and Nussbaum, 1994a).

A general herpetological survey of the recently established Ranomafana National Park in eastern Madagascar (hereafter, RNP; Fianarantsoa Province, Ifanadiana fivondronana; Fig. 3) has resulted in discovery of a number of new species of amphibians and reptiles (e.g., Cadle, 1995). The primary aim of this paper is to clarify the status of species of *Liopholidophis* from the RNP. In doing so, I describe two new species, resurrect two old names from synonymy, and summarize data for the other species. A full-scale revision of *Liopholidophis* is beyond the scope of this report, but I have undertaken revisionary steps pertinent to the nomenclature of species occurring in the RNP, which includes all species recognized herein except *pinguis* and *stumpffi* (Boettger) (see later). Some questions concerning species limits within *Liopholidophis*, especially in the broadly distributed species *lateralis* and *sexlineatus*, clearly need to be examined anew with more detailed geographic comparisons than undertaken here.

I summarize knowledge of all species, present illustrations (except *stumpffi* and *pinguis*) and descriptions of hemipenes of all species, and hypothesize relationships within the species groups based on external morphology, color patterns, hemipenes, skull morphology, and behavior. Revised synonymies are given for all species. Nomenclaturally relevant actions taken herein include the following. (1) *Dromicus doliocercus* Peracca (1892) is resurrected

from the synonymy of *Liopholidophis sexlineatus* (Günther), where it was placed by Guibé (1958). (2) A lectotype is designated for *Dromicus stumpffi* Boettger, a species known only from northern Madagascar (at least Nossi-bé, the type locality, and the vicinity of Montagne d'Ambre); a wide-ranging species of the eastern forests previously confused with *stumpffi sensu* Boettger is described as new. (3) A lectotype is designated for *Ptyas infrasignatus* Günther (1882), and that name is recognized as a senior synonym of *Liopholidophis thieli* Domergue (1973), as used widely in current literature (e.g., Glaw and Vences, 1994).

## MATERIALS AND METHODS

My study of *Liopholidophis* is based primarily on specimens resulting from a herpetofaunal survey of the RNP. In reviewing the species of the RNP, I incorporate data from other specimens (Appendix) and from the literature as necessary. I have not attempted a comprehensive survey of museum specimens or a thorough study of geographic variation in any species, although I comment where appropriate on apparent geographic patterns. I have probably seen most known specimens of *doliocercus*, *grandidieri*, *pinguis*, and *rhadinæa*, new species.

Distributional summaries are based on specimens examined (Appendix), Domergue (1973), and Parker (1925). However, I have not verified the identity of specimens at the limits of the ranges for the widespread species *epistibes*, new species, *lateralis*, and *infrasignatus*; the literature and localities documenting those limits are cited in the species accounts. Most natural history observations are from the RNP region, although for the widespread species *L. sexlineatus* and *L. lateralis*, I have included observations from other localities. Such instances are identified in the text. Comments on general macrohabitats of prey items (e.g., "arboreal") are from personal observations and, unless otherwise stated, are from the RNP and of active animals; of course, the snakes could

<sup>2</sup> Virtually all authors, apparently beginning with Jan (1863) and Boulenger (1893), have cited authorship of this name as "Duméril and Bibron," but the species is described in volume 7 of the *Érpetologie Générale*, authored by Duméril, Bibron, and Duméril.

likely have captured inactive prey, whose retreat sites are less well known.

For convenience I refer to the two species groups erected by Parker (1925), modified to reflect my view of their composition, as follows: (a) the *sexlineatus* group: *sexlineatus*, *dolicocercus*, *grandidieri*, *pinguis*, and *rhadinaea*, new species; and (b) the *stumpffi* group: *stumpffi*, *infrasinatus*, *lateralis*, and *epistibes*, new species. Additional justification for these groups is given later (see "Monophyly of the Species Groups of *Liopholidophis*").

Hemipenial terminology follows Myers (1973, 1974), Myers and Campbell (1981), and Myers and Cadle (1994). All everted organs were inflated with colored jelly to enhance the surface ornamentation prior to description. In several cases identified below I used a modification of the method of Pesantes (1994) for preparing everted organs from hemipenes originally preserved partially or wholly inverted. However, rather than neutralization of the potassium hydroxide (KOH) treatment with hydrochloric acid, as in Pesantes (1994), I exhaustively soaked the organs in several changes of water followed by several changes of alcohol. This was to avoid possible damage to calcified structures by the acid treatment. The method works well, although it is easy to puncture small, delicate organs. However, as a cautionary note, hemipenes everted in this way may not assume precisely the same form as organs everted from fresh specimens unless the KOH treatment is sufficient to assure complete expansion of the soft tissue (see description of *Liopholidophis stumpffi* hemipenis, later). In my limited experience, the method works better for larger organs than for smaller ones, which are inherently more delicate (hence, I tended to be conservative in application of the KOH treatment). Descriptions of hemipenial morphology and skull osteology are relegated to comprehensive sections apart from species accounts.

Inferences of reproductive mode were confirmed, where possible, according to criteria and terminology outlined by

Blackburn (1993, 1994). Museum abbreviations used in the text are given at the beginning of the Appendix. Translations from French and Italian are my own; Malagasy names for snakes are translated when their meaning seems evident.

Coordinates for localities are given in the text where pertinent and for all localizable localities in the Appendix. Unless otherwise stated, coordinates were derived from three principal sources: (1) for localities in the vicinity of the RNP, the series of 1:50,000 maps published by the Foiben-Taosarintanin'i Madagasikara, Antananarivo (FTM); (2) a series of four 1:1,000,000 maps of Madagascar, also published by the FTM; and (3) the Defense Mapping Agency (1989) gazetteer. Specific localities within the RNP are mapped in Cadle (1995). A useful discussion of some historical Malagasy collections and localities is given by Carleton and Schmidt (1990), and Glaw and Vences (1994:appendix 7) give an abbreviated list of herpetological localities.

Malagasy place names are notoriously redundant and highly variable in their spellings (e.g., Nossi-bé, Nosy Be, and Nosisé for the island properly referred to as Nosy Be ["Big Island"]). Most names of the colonial period are now reverting to their traditional ones (e.g., Diego Suarez = Antsiranana; Tamatave = Toamasina). In quoting localities from original sources (e.g., publications, museum catalogs), I use the spelling variants in those sources but give a modern equivalent at least upon the first use; localities are heavily annotated in the Appendix to facilitate cross-referencing.

## DESCRIPTIONS OF TWO NEW SPECIES

The first new species to be described is a member of the genus *Liopholidophis* Mocquard (1904:302–304) by virtue of having strong sexual dimorphism in tail length (>35% of total length in males, <30% in females), 17 midbody scale rows (reducing to 15 posteriorly), hypapophyses present on posterior trunk vertebrae, maxillary teeth 23–28 + 2 ungrooved fangs,



Figure 1. *Liopholidophis rhadinaea*, holotype (MCZ 180395, male). Approximately  $\times 0.9$ .

smooth scales without apical pits, deeply bilobed hemipenis ornamented with spines, and a deeply bifurcate centrolineal sulcus spermaticus. The relative tail lengths in the two sexes, in combination with having 17 midbody scale rows, ally the new species to the *sexlineatus* group of *Liopholidophis* (Parker, 1925). However, as suggested later (see "Monophyly of *Liopholidophis*"), little evidence supports the monophyly of *Liopholidophis* broadly conceived, and future reevaluation of the status of all included species is warranted.

*Liopholidophis rhadinaea*,  
new species

Figures 1–2, 4–5

*Liophidium* sp.: Domergue (1988:144, specimen 2).

**Holotype.** Museum of Comparative Zoology (MCZ) 180395 (field number JEC 11466), an adult male in good condition (Figs. 1–2) from Talatakely, Ranomafana National Park, 950–1,000 m, Fivondronana Ifanadiana, Fianarantsoa Province,

Madagascar [ $21^{\circ}16'S$ ,  $47^{\circ}25'E$ ]. Specimen obtained by John E. Cadle 20–26 December 1991.

**Paratypes.** Eighteen specimens, 17 in the Museum of Comparative Zoology obtained by J. E. Cadle, one in the Museum National d'Histoire Naturelle, Paris (MNHN). All specimens in the MCZ are paratopotypes; data for the MNHN specimen are given below: **MCZ 180385** (field number JE Cadle 9644), adult female, 26 October 1990; **MCZ 180386** (JEC 9649), adult female, 24 October 1990; **MCZ 180387** (JEC 9932), hatchling female,<sup>3</sup> 19 November 1990; **MCZ 180388** (JEC 9933), subadult female, 19 November 1990; **MCZ 180389** (JEC 10087), adult male, 25–28 November 1990; **MCZ 180390** (JEC 10115), adult male, 4 December 1990; **MCZ 180391** (JEC 10152), adult female, 9 December 1990; **MCZ 180392** (JEC 10610),

<sup>3</sup> Specimens  $\leq 135$  mm SVL were considered hatchlings.



Figure 2. *Liopholidophis rhadinaea*, head of MCZ 180395 (holotype). Approximately  $\times 5$ .

adult male, 15 November 1990; **MCZ 180393** (JEC 11180), adult female, fluid + cleared and stained skull, 17 December 1991; **MCZ 180394** (JEC 11223), adult male, 18 December 1991; **MCZ 180396** (JEC 11564), adult male, 2 January 1992; **MCZ 180397** (JEC 11575), adult female, 3 January 1992; **MCZ 180398** (JEC 11576), hatchling female, 3 January 1992; **MCZ 180399** (JEC 11891), adult female, 11 December 1992; **MCZ 180400** (JEC 12344), adult female, 1 January 1993; **MCZ 180401** (JEC 12385), adult female, 5 January 1993; **MCZ 180402** (JEC 12388), adult male, 5 January 1993.

**MNH 1988-333** (field number 717/S), collected 14 January 1966 by M[ichel] Vincke<sup>4</sup> "north of Bevatraka, and 22 km north of the terminus of the Perinet forestry railroad" [Toamasina Province, Fivondronana Moramanga] (data translated from field tag attached to specimen). Perinet (=Andasibe) is at about 900 m on the eastern escarpment [18°56'S, 48°25'E]. This specimen was discussed as *Liophidium* sp. by Domergue (1988:144, specimen 2), who gave the identical locality except that the initial phrase was reported as "forêt de Bevotaka." I have been unable to locate either *Bevotaka* or *Bevatraka* in gazetteers or on maps, although Perinet itself is well

known. Domergue (1988) erroneously reported the midbody dorsal scale count for this specimen as 15, rather than the 17 that it has.

*Distribution.* Known only from the type locality, Talatakely, within the RNP (21°16'S, 47°25'E), and from near "Bevatraka," 22 km N of Perinet (=Andasibe; 18°56'S, 48°25'E) (Fig. 3). The known elevational range is approximately 950–1,100 m at the type locality.

*Etymology.* The specific epithet is a noun in apposition referring to the Neotropical snake genus *Rhadinaea*, many species of which are strikingly similar to *Liopholidophis rhadinaea* in habitus, coloration, pattern, and montane forest habitat. The name also alludes to the characteristic slenderness of both *L. rhadinaea* and species of *Rhadinaea* (from the Greek proper name *Rhadine*, itself derived from *rhadinos* [=slender, lithe; see Myers, 1974: 16, 19]).

*Diagnosis.* *Liopholidophis rhadinaea* differs from all other members of the genus by the following combination of features: dorsal scales in 17–17–15 rows; tail 37–43% of total length in males, 24–27% in females; small size and slender habitus (largest known male 749 mm total length, largest known female 424 mm total length); ventrals 170–179 in males, 150–160 in females; subcaudals 126–135 in males, 69–77 in females; usually 8 upper labials (but high frequency of 7); 8 or 9 lower labials; and pattern consisting of three light yel-

<sup>4</sup> Listed as "M. Vincke" on the field tag, this is assumed to be the Michel Vincke who collected the type of *Geodipsas vinckei*, as reported by Domergue (1988:140).

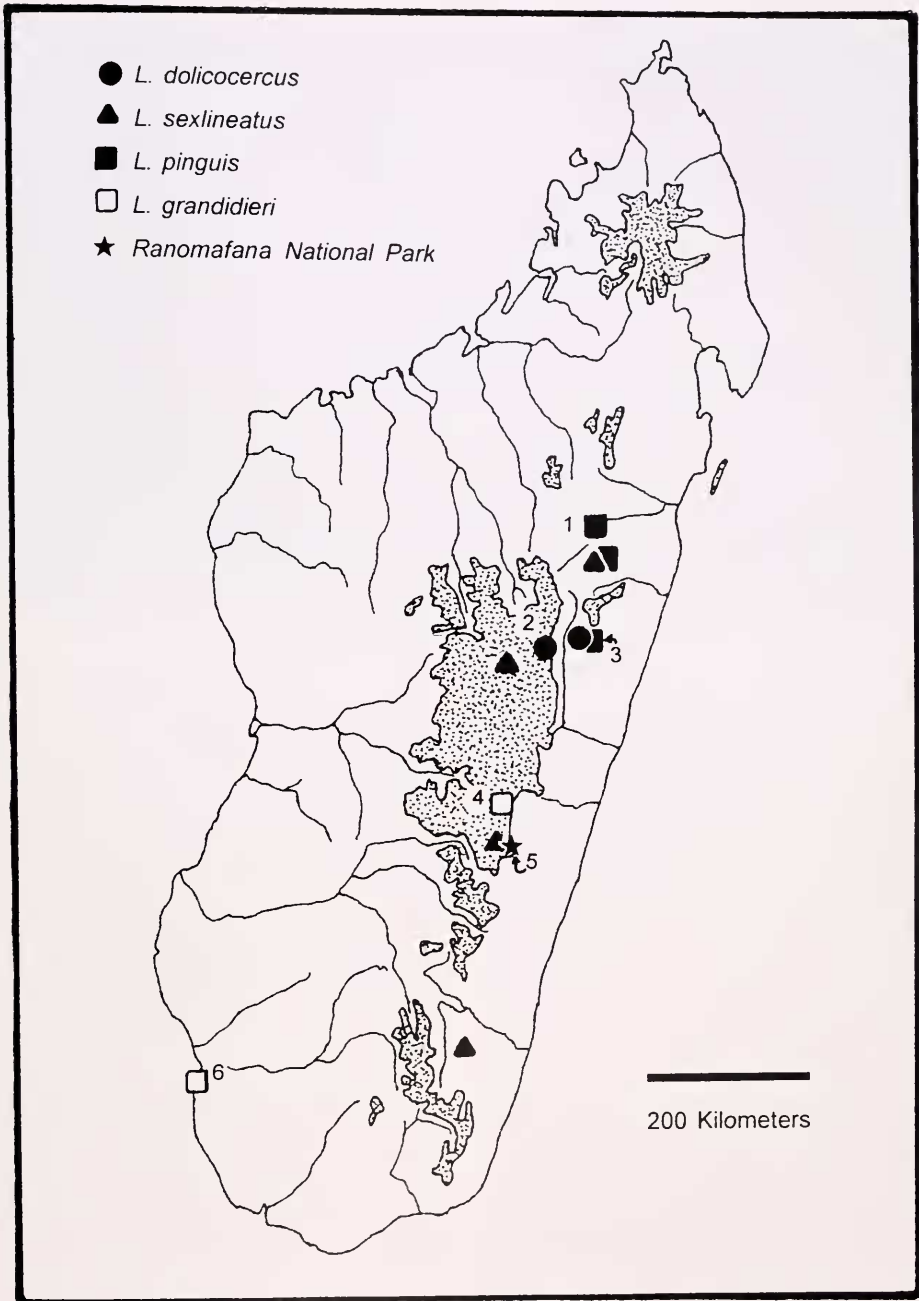


Figure 3. Distribution of species of the *Liopholidophis sexlineatus* group; shaded areas are above 1,000 m. All species indicated except *pinguis* are known from the RNP (locality 5). *Liopholidophis rhadinaea*, new species, is known from localities 5 (type locality) and 3. All known localities for species other than *sexlineatus* are indicated (see text for known distribution, and Glaw and Vences [1994:338] for a more comprehensive map of *sexlineatus* localities). Localities referred to in the text and Appendix are numbered as follows: (1) "Antsihanaka," type locality for *L. pinguis* Parker; (2) Andrangoloaka, type locality for *L. doliocercus* (Peracca); (3) Perinet [Andasibe]; (4) Ambohimombo; (5) RNP; and (6) Saint Augustine Bay, type locality [in error] for *L. grandidieri* Mocquard.

lowish brown nape spots (Fig. 2), broad dark brown stripe occupying middorsal 3 to 5 scale rows, narrow light yellowish brown dorsolateral stripes centered on scale rows 6 (anteriorly) or 5 (posteriorly), dark brown line on dorsal row 1, and light venter (pink to vermilion in life) (see Figs. 1, 4, 5).

*Liopholidophis rhadinaea* differs from species of the *stumpffi* group in having 17–17–15 scale rows and strong sexual dimorphism in tail length (19–19–17 scale rows and no strong dimorphism in tail length in the *stumpffi* group).

Four previously described valid nominal species of *Liopholidophis* (*dolicocercus*, *grandidieri*, *pinguis*, *sexlineatus*; cf. Table 1) have 17–17–15 rows, but all are larger and more robust than *L. rhadinaea*. *Liopholidophis dolicocercus* (to 928 mm total length in males, 992 mm in females) has fewer ventrals in both sexes (156–157 in males, 143–150 in females) and more subcaudals in males (140–164), has a distinctively patterned black venter bordered laterally with white stripes, and lacks discrete stripes on the dorsum. *Liopholidophis grandidieri* (to 1,636 mm total length in males, 674 mm in females) has a black venter, lacks distinct middorsal dark and dorsolateral light stripes (yellowish brown to yellow middorsal area heavily suffused with black or dark brown; lateral dark stripe on rows 2 + 3), and has a longer tail with more subcaudals in both sexes (tail >50% of total length and >200 subcaudals in two males; 35% of total length and 98+–113 subcaudals in two females). *Liopholidophis pinguis* (to 890 mm total length in males, 685 mm in females) has an olive dorsal ground color with dark stripes (sometimes indistinct) and lacks light nape spots; males of *pinguis* have fewer ventrals (151–154), a shorter tail (33% of total length), and fewer subcaudals (91–98) than males of *rhadinaea*. *Liopholidophis sexlineatus* (to 1,338 mm total length in males, 726 mm in females) differs from *L. rhadinaea* in having fewer ventrals (148–163 in males, 139–148 in females), having an olive dorsal ground color with black stripes,

lacking light nape spots, and having a whitish belly that may be heavily suffused or mottled with black.

*Liophidium rhodogaster* is sympatric with *Liopholidophis rhadinaea* at the two known localities for the latter and is very similar in overall appearance, including dorsal pattern and (in life) pink venter (this resemblance was noted by Domergue [1988] in discussing MNHN 1988-333, which he considered an undescribed species of *Liophidium*; cf. Figs. 1 and 5 with Glaw and Vences [1994:pl. 339]). *Liophidium rhodogaster* differs from *Liopholidophis rhadinaea* in lacking dorsal scale row reductions (17–17–17), having more ventrals (184–212 in the RNP), lacking extreme sexual dimorphism in relative tail length, and having a shorter tail in general (18–23% of total length, sexes combined). Additional comparisons of *rhadinaea* with *Liophidium* are given later (Discussion).

*Data on the Holotype (MCZ 180395).* The holotype is an adult male with everted hemipenes. Total length 720 mm; tail length 308 mm (43% of total length). Greatest head width (parietal region) 5.85 mm, head length 11.4 mm from tip of snout to end of mandibles. Dorsals 17–17–15, the reduction occurring by fusion of rows 3 + 4 at the level of ventral 105. Three preventrals, 179 ventrals, divided anal plate, 126 pairs of subcaudals. 8–8 supralabials (4–5 touching eye), 9–9 infralabials, 1 + 2 temporals on each side. Weight in life 15 g.

*Description.* Measurements, proportions, and scutellation are summarized in Table 1. Largest specimen a male (MCZ 180392), 749 mm total length, 320 mm tail length; largest female (MCZ 180399) 424 mm total length, 115 mm tail length. Tail length strongly sexually dimorphic: 37–43% of total length in males, 24–28% of total length in females. Dorsal scales smooth, lacking apical pits, in 17–17–15 rows. Scale row reduction from 17 to 15 rows usually by fusion of rows 3 + 4 (occasionally appearing as loss of row 4) at the level of ventrals 86–113 (males, N = 7) or 78–96 (females, N = 11) (2 individ-





Figure 4. *Liopholidophis rhadinaea*, MCZ 180394 (male), in life.

uals had unilateral reduction of 4 + 5 on one side and 3 + 4 on the other). Ventrals 170–179 in males, 150–160 in females. Anal plate divided. Subcaudals 126–137 in males, 69–88 in females (88 subcaudals in MNHN 1988-333; maximum of 77 in the RNP series).

Rostral slightly visible from above, about 2 times wider than high. Paired internasals, each slightly wider than long, about 80% as long as prefrontals. Paired prefrontals, each wider than long, in contact with each other and with frontal, supraocular, preocular, loreal, postnasal, and internasal. Frontal roughly pentagonal (sometimes with a slightly angulate anterior border, producing a more hexagonal shape), 1.1–1.3 times longer than its greatest width (at frontal/prefrontal suture), 1.1–1.2 times longer than distance from its anterior edge to tip of snout. Parietals about 1.5 times longer than broad; interparietal suture about 70% length of frontal plate. Nasal divided ventral to nostril, in contact with rostral, internasal, prefrontal, loreal, and first 2 supralabials. Loreal rectangular to pentagonal, usually higher than wide,

separated from eye by single preocular (unilateral transverse division of preocular in 3 specimens). Two postoculars; temporals 1 + 2. Supralabials usually 8 with 4–5 touching eye (11 specimens), or 7 with 3–4 touching eye (5 specimens) (1 specimen each with 7–8 and 7–6). Infralabials 8–8 (6 specimens), 8–9 (2 specimens), or 9–9 (10 specimens), the first pair in contact behind the mental, 1–4 touching an anterior genial, 4–5 touching a posterior genial (1 specimen with 1–3 and 3–4, respectively). Anterior genials approximately equal to, or slightly shorter than, posterior genials. Scattered minute pits or tubercles visible on head plates of some specimens under high magnification, especially on circumorbital series, prefrontals, and nasals.

Overall body form slender, gracile (Fig. 4). Body higher than wide; ventrolateral edge of body angulate. Head very slightly wider than neck. Pupil round. Eye moderate, its diameter 60–65% of the distance from anterior edge of eye to tip of snout; eye diameter 1.2 times the distance from eye to posterior edge of nostril.

Posterior hypapophyses, examined *in situ*, appear to be a more or less rectangular vane, with a posterior projection that does not, or only barely, overlap the centrum of the next vertebra.

*Dentition.* Maxillary teeth 22–28 + 2 ( $\bar{x}$  = 23.9 ± 1.81; N = 16). Modal number of prefang teeth 23 (N = 7), followed by 24 (N = 3), 22 or 25 (N = 2 each), and 28 (N = 2). Essentially no diastema. The ungrooved fangs are about twice as large as the posteriormost maxillary teeth and have a rounded anterior surface and a flattened knifelike posterior surface; their tips are slightly compressed. The ultimate fang is very slightly offset laterad, but the fangs are essentially in line with the tooth row. A cleared and stained skull (MCZ 180393, female) has 16–15 palatine teeth, 25 right pterygoid teeth, and 28 right dentary teeth (left pterygoid and dentary damaged).

*Hemipenis* (see Fig. 30). Deeply bilobed, noncapitate, acalyculate (ornamentation consists entirely of spines), with small, nude, cylindrical awns at the tips of the lobes. Stalk of organ proximal to lobes moderately long (about 40% the length of the organ). Sulcus spermaticus deeply bifurcate, centrolinal, with the tips funnel-shaped and opening at the base of the awns. The awns are a very unusual feature of the hemipenes, which are described in detail later (see “Hemipenial Morphology in *Liophilidophis*”).

*Coloration in Life.* Two similar but distinct color morphs are evident. Most specimens from the RNP, and the specimen from Perinet, are a “light” morph; three RNP specimens (MCZ 180385–86, 180388) are a “dark” morph described separately. The two forms differ primarily in the width of the dorsal dark brown stripe and in the shade of the brown flank coloration.

“Light” morph in life, based on MCZ 180392 (male) (Fig. 5)—Dorsum brown, including broad dark brown stripe occupying median 3 dorsal rows + ½ of adjacent rows, bordered by narrow yellowish brown dorsolateral stripe (centered on row 6 + approximately ⅓ or less of adjacent

scale rows); flanks medium yellowish brown; dark brown line on lower portion of scale row 1. Top of head brown, without darker patterns. A median and a pair of dorsolateral yellowish brown nape spots. Upper and lower labials and throat whitish with some darker stippling. Anterior 10–15 ventrals whitish. Remainder of ventrals, anal plates, and subcaudals salmon pink with a few scattered dark brown specks. Dorsal and ventral patterns continue to tail tip.

“Dark” morph in life, based on MCZ 180385–86 (females) (Fig. 5)—Broad dark brown stripe occupying median 5 dorsal rows, bordered by narrow yellowish brown stripe from nape to tail tip (centered on row 6 + approximately ⅓ or less of adjacent scale rows). Flanks dark brown, of a shade somewhat lighter than the middorsal dark stripe. A somewhat irregular thin dark brown line on lower half of scale row 1 (manifested posteriorly in MCZ 180385 as a series of irregular spots at the juncture of the ventral plates and scale row 1). Three yellowish brown spots on nape. Top and sides of head brown. Upper and lower labials white, speckled with dark grayish or brownish. Throat and anterior ventrals white with some dark pigment on edges of scales. Most ventrals vivid salmon pink with some dark specks laterally. Subcaudals bright salmon pink.

In the “dark morph,” the dark flank coloration occupies the lower 4½ dorsal rows anteriorly, dropping to the lower 3½ rows posteriorly. Under magnification, these scales are heavily stippled with dark brown, giving a uniform appearance when viewed by eye. In the “light morph,” the flanks (first 5 dorsal rows anteriorly, first 4 posteriorly) are medium to light brown; under magnification, these scales are light brown, lightly stippled with dark brown. Two specimens, MCZ 180391 and 180400, are somewhat intermediate between the “light” and “dark” morphs: they have a narrow dark middorsal stripe (i.e., 3 rows wide), but their flanks (in preservative) are of a brown shade intermediate between typical specimens of the “light” and “dark”

morphs. The light dorsolateral stripes vary somewhat in width, the variation due to the proportional involvement of rows 5 and 7 in the stripe (from marginal involvement to approximately  $\frac{1}{2}$  of each scale).

Although ventral pinkish pigmentation is often variably present in many snakes with otherwise immaculate venters, the pink coloration on the venter of *Liopholidophis rhadinaea* is a constant, usually vivid, feature of all specimens. The hue varies from a rather plain pink to brilliant vermillion. In its most vivid manifestation, the ventral color of *L. rhadinaea* does not match the brilliant electric hue of the similar sympatric species, *Liophidium rhodogaster*. Most specimens have a small dot of dark brown pigment at the extreme lateral edges of the ventral plates; this pigment is more extensive in MNHN 1988-333, in which the ventral plates have distinct darkened borders, than in the RNP sample. Many specimens have additional irregular scattered dark brown flecks on the venter, occasionally arranged in a pair of lines flanking the ventral midline on part of the belly.

**Coloration in Preservative.** Rostral and upper labials mostly white (some fine dark brown stippling, especially on rostral and anterior supralabials). Thin dark blackish line separating whitish upper labial color from the brown head cap; beginning at tip of snout about midlevel on the rostral, extending across upper border of supralabials 1-4, thence across lower edge of ventral postocular and anterior temporal, and across upper  $\frac{1}{3}$ - $\frac{1}{2}$  of last two upper labials, ending at corner of mouth. In some specimens the lower portion of the supralabials are also stippled with dark pigment, so that the white of the upper lip is essentially sandwiched between dark lines. Top of head brown, slightly lighter than middorsal dark stripe, lightly stippled with dark under magnification, but essentially patternless. Throat immaculate.

Three light nape spots (Fig. 2); lateral ones usually separated from light color of throat by surrounding brown pigment (brown head cap laterally continuous with



Figure 5. *Liopholidophis rhadinaea*, two color morphs. Top: Specimen of the "light" morph (MCZ 180400). Bottom: Specimen of the "dark" morph (MCZ 180385). Note the darker flanks in the latter and its narrower dorsolateral light stripe.

brown color of flanks); lateral nape spots confluent with light color of throat in six specimens. Nape spots bordered completely or incompletely by thin dark brown line.

Middorsal stripe dark brown. Dorsolateral light stripes dirty whitish to dirty yellowish brown, bordered with thin dark brown line (sometimes incomplete along ventral edge). In some specimens of both color morphs, dorsolateral light stripes essentially restricted to scale row 6 (e.g., MCZ 180386, 180396). Light stripes in line with,

but separated from, lateral nape spots by a brown collar about 2–3 scales wide. The light stripes continue to the tail tip and are not interrupted in the region of the vent.

Dark brown line on lower half of dorsal row 1, sharply separating dorsal and ventral ground colors, occasionally indistinct; interrupted briefly at the vent, then continuing at extreme lateral edge of subcaudal scales to tail tip (subcaudals otherwise immaculate). Venter dull whitish to yellowish white, depending on time in preservative (pink pigmentation lost), except for the persistent brown dots.

*Natural History.* *Liopholidophis rhadinaea* is diurnal and terrestrial. Most specimens were encountered while actively crossing trails or (occasionally) apparently sunning on trails. Specimens were collected from selectively logged rainforest that, however, still had a closed canopy and was deeply shaded (essentially as primary forest) in most parts.

These are inoffensive little snakes and do not attempt to bite. One specimen encountered on a trail used immobility as a defense, flattening its body against the trail and maintaining rigidity; it did not even move initially (even remaining rigid) when prodded or picked up. One specimen attempted to take refuge inside a broken bamboo stem close to the ground.

Two diet records are available for *Liopholidophis rhadinaea*, both frog eggs. A male collected early in the afternoon of 18 December 1991 (MCZ 180394) regurgitated a freshly consumed mass of frog eggs, including 16 more or less intact, plus fragments of 1–3 others. The eggs were non-pigmented with yellowish yolk and a gelatinous capsule. Capsule diameters of the formalin-preserved eggs were 10–12 mm, with the ova 3–3.5 mm. These eggs appeared similar to those of *Plethodontohyla inguinalis* (Microhylidae) observed in the RNP. That species lays clutches in tree holes (Altig and Cadle, unpublished data), often close to the ground, where they might be accessible to a terrestrial snake such as *L. rhadinaea*. Of course, the identity of the egg clutch remains uncertain, but it

seems most likely to be one of the larger cophyline microhylids (*Platypelis*, *Plethodontohyla*), because these seem to be the only frogs with such large eggs in the RNP (personal observations). Frogs, especially microhylids, appear to be primary dietary items of other forest species of *Liopholidophis* in the RNP (see species accounts). Another male collected 6 December 1990 (MCZ 180390) at 1100 hr. contained four intact egg yolks similar in color, size, and consistency to those described for the previous specimen.

*Liopholidophis rhadinaea* is oviparous. Females apparently begin yolking follicles late in the dry season in the RNP: two females collected 24 and 26 October (MCZ 180385–86) had small yolking follicles. All adult females collected during the rainy season (actual dates 9 December to 14 January, including MNHN 1988–33 from Perinet) had two (four females) or three (four females) well-yolked eggs; eggs in females collected 9–17 December were unshelled oviductal eggs, whereas those collected 1–14 January all contained shelled eggs. One embryo from MCZ 180401 (collected 5 January) was in Zehr (1962) stage 21–22. Females with yolking follicles or eggs were 262–313 mm SVL. Three small juveniles with umbilical scars (162–225 mm total length; 122–170 mm SVL) were collected on 19 November and 3 January.

In the RNP, *Liopholidophis rhadinaea* is broadly sympatric with the following species of *Liopholidophis*: *lateralis*, *epistibes*, new species, *infrassignatus* (“*thieli*”), *grandidieri*, *dolicocercus*, and *sexlineatus*. Of these, all except *lateralis*, *grandidieri*, and *sexlineatus* are known to be microsympatric with *rhadinaea* (i.e., to occur in the closed-canopy forest habitat where all specimens of *rhadinaea* have been collected). In the RNP, *lateralis* tends to occur in more open habitats, whereas *sexlineatus* prefers marshy to aquatic habitats, and is especially common in rice paddies; *grandidieri* is known from the RNP by a single specimen collected atop a granite massif with rather open habitats (additional comments later). At Perinet, *rhad-*

*inaea* is broadly sympatric with at least the following species of *Liopholidophis*: *epistibes*, new species, *lateralis*, *infrasingnatus* ("thieli"), *sexlineatus*, and *pinguis* (Domergue, 1973; Glaw and Vences, 1994; Appendix).

## Discussion

The superficial similarity of *Liopholidophis rhadinaea* to some species of *Liopholidium* is striking, leading Domergue (1988:specimen 2, p. 144) to refer one of the paratypes of *rhadinaea* to "*Liopholidium* sp." In fact, *Liopholidophis rhadinaea* superficially resembles some species of *Liopholidium* (e.g., *rhodogaster*, *torquatium*) much more than it does other species of *Liopholidophis*. Hence, it seems worthwhile to explore more fully the characters that *rhadinaea* shares with both genera. A detailed consideration of the relationships of *rhadinaea* within *Liopholidophis* is deferred until species accounts and detailed hemipenial descriptions of other species are given.

Strong sexual dimorphism in tail length, an unusual and unquestionably derived character within colubrids, is the most obvious characteristic indicating the relationship of *rhadinaea* to *Liopholidophis* (specifically, to the *sexlineatus* group, for which the character is here interpreted as a synapomorphy; additional comments later). Of the more than 65 species of Malagasy colubrids, only species of the *Liopholidophis sexlineatus* group show no overlap between the sexes in the relative tail length compared to the total length; in all species of the *sexlineatus* group except *pinguis*, the tail of males is >35% of total length (averages >40%; see Table 1). In addition, *Liopholidophis rhadinaea* shares other osteological, scutellational, and pattern characteristics with members of the *sexlineatus* group (see "Monophyly of the Species Groups of *Liopholidophis*"). On the other hand, hemipenial morphology is rather heterogeneous in the *Liopholidophis sexlineatus* group (see "Hemipenial morphology in *Liopholidophis*");

the hemipenis of *rhadinaea* is no more dissimilar to other members of that group than, for example, are the organs of *dolicocercus* compared to either *grandidieri* or *sexlineatus*.

In contrast to the tail synapomorphy shared between *rhadinaea* and species of the *Liopholidophis sexlineatus* group, no special similarities are obvious between *Liopholidophis rhadinaea* and *Liopholidium*. Although synapomorphies for *Liopholidophis sensu lato* have not been identified, some species of *Liopholidium* have derived skull and dentitional characters associated with feeding on hard-bodied lizard prey such as skinks and cordylids (Savitzky, 1981, 1983). *Liopholidophis rhadinaea* shows none of these derived features, which include the following (contrasting characteristics of *L. rhadinaea*, based on the cleared and stained skull of MCZ 180393, in parentheses): (1) basal hinge allowing teeth to fold toward the back of the mouth (teeth firmly ankylosed to jaws); (2) teeth short, blunt, and often spatulate (teeth sharp, curved, and not short); (3) compound bone of lower jaw strongly curved and articulating far forward, near the anterior end of the dentary (compound bone curved only at tip of the mandible, articulating on the posterior half of the dentary); and (4) long, free posterior dentigerous process on the dentary (posterior dentigerous process not especially long).

Morgan (1973) reviewed *Liopholidium* and compared skulls of four species (*mayottensis*, *rhodogaster*, *vallanti*, *torquatium*). An unusual feature of the premaxilla shared by these species was the presence of long lateral processes that overlap the anterolateral surfaces of the maxillae (confirmed by my study of a skull of *L. rhodogaster* [JEC 11571] and photographs of skulls of *mayottensis*, *rhodogaster*, and *vallanti* in Morgan [1973]). In contrast, the premaxilla and maxillae of *Liopholidophis rhadinaea* are separated by a moderate gap, which seems to be the common condition in *Liopholidophis* (eight other species examined, of which the premaxilla and maxilla overlapped in *sexlineatus* only;

see "Osteological Comparisons" for specimens examined).

I also compared everted hemipenes of *Liopholidophis rhadinaea* to those of *Liophidium rhodogaster* and *Liophidium torquatum*. The hemipenes of these *Liophidium* species are deeply bilobed and spinose, as is the hemipenis of *rhadinaea*, but otherwise no special resemblances are shared between organs of *rhadinaea* and the other two. However, as a cautionary note, the organs of *L. rhodogaster* and *L. torquatum* are rather different from one another (e.g., basal naked pocket and lobes in *torquatum*, absent in *rhodogaster*; personal observations), and they are different from descriptions and figures of three other species given by Domergue (1983). Since hemipenial variation in *Liophidium sensu lato* remains unstudied, the significance of such differences will only be understood as the hemipenial morphology of it and other Malagasy colubrid genera is comprehended.

Finally, Domergue (1969:15) suggested another "key" character to distinguish species of *Liophidium* from *Liopholidophis*: venter violaceous, red, or pinkish with regular spotting in the former; yellowish to whitish with irregular spotting in the latter. Clearly, *Liopholidophis rhadinaea*, in having a pink to vermilion venter, is an exception to this generality and exceptional among species of *Liopholidophis* in this characteristic.

Given current definitions and limits for Malagasy colubrid genera, *Liopholidophis* is the most appropriate genus for *rhadinaea*. Nevertheless, this is not an unequivocal generic placement. Despite a long list of similarities, some of them putatively derived, between *rhadinaea* and the *sexlineatus* group of *Liopholidophis* (see "Monophyly of the Species Groups of *Liopholidophis*"), the disturbing lack of clear synapomorphies for *Liopholidophis sensu lato* (discussed later) makes resolution of this question problematic. Furthermore, the diversity within *Liopholidophis*, the disparity in general habitus between *rhadinaea* and the other species, and the re-

semblances (albeit superficial) between *rhadinaea* and species of *Liophidium*, all convene to raise questions concerning the relationships of *rhadinaea*. My cursory comparisons of *Liophidium* species in connection with this study raise similar questions for that genus, especially concerning variation in hemipenes and some of the dentitional and cranial characteristics already alluded to. The possibility of a close relationship between *Liophidium* and *Liopholidophis*, or parts thereof, should be evaluated as knowledge of species in each genus improves. (See also the subsequent section on MNHN 1988-331.)

The next species described has been confused with *Liopholidophis stumpffi* (Boettger, 1881a,b) in previous literature (Boulenger, 1893; Boettger, 1913; Domergue, 1973; Glaw and Vences, 1994). Domergue (1973) properly resurrected *Dromicus stumpffi* Boettger (1881a,b) from the synonymy of *Liopholidophis lateralis*, where it had been placed in previous general reviews of *lateralis* (Guibé, 1954, 1958). However, Domergue, as had others before (e.g., Boulenger, 1893; Boettger, 1913; Kaudern, 1922; Parker, 1925; Angel, 1936), confused a wide-ranging species of eastern and northern Madagascar with *L. stumpffi* (Boettger) (Domergue, 1973:fig. 1; followed by Glaw and Vences, 1994:336 [map]). My examination of type material of *Dromicus stumpffi* Boettger, other topotypic specimens, and specimens from eastern Madagascar referable to *Liopholidophis stumpffi sensu* Domergue (1973) convinces me that two taxa are involved. Accordingly, *Liopholidophis stumpffi* (Boettger) is here considered a species of the type locality (Nosy Be) and extreme northern Madagascar (Fig. 6). Populations previously confused with *stumpffi* Boettger (i.e., from the eastern escarpment and lowlands, the vicinity of Mahajanga in northwestern Madagascar, and Montagne d'Ambre in extreme northern Madagascar) are described as a new species. Distributional relationships between the new species and true *stumpffi* are unclear (see "Distribution").

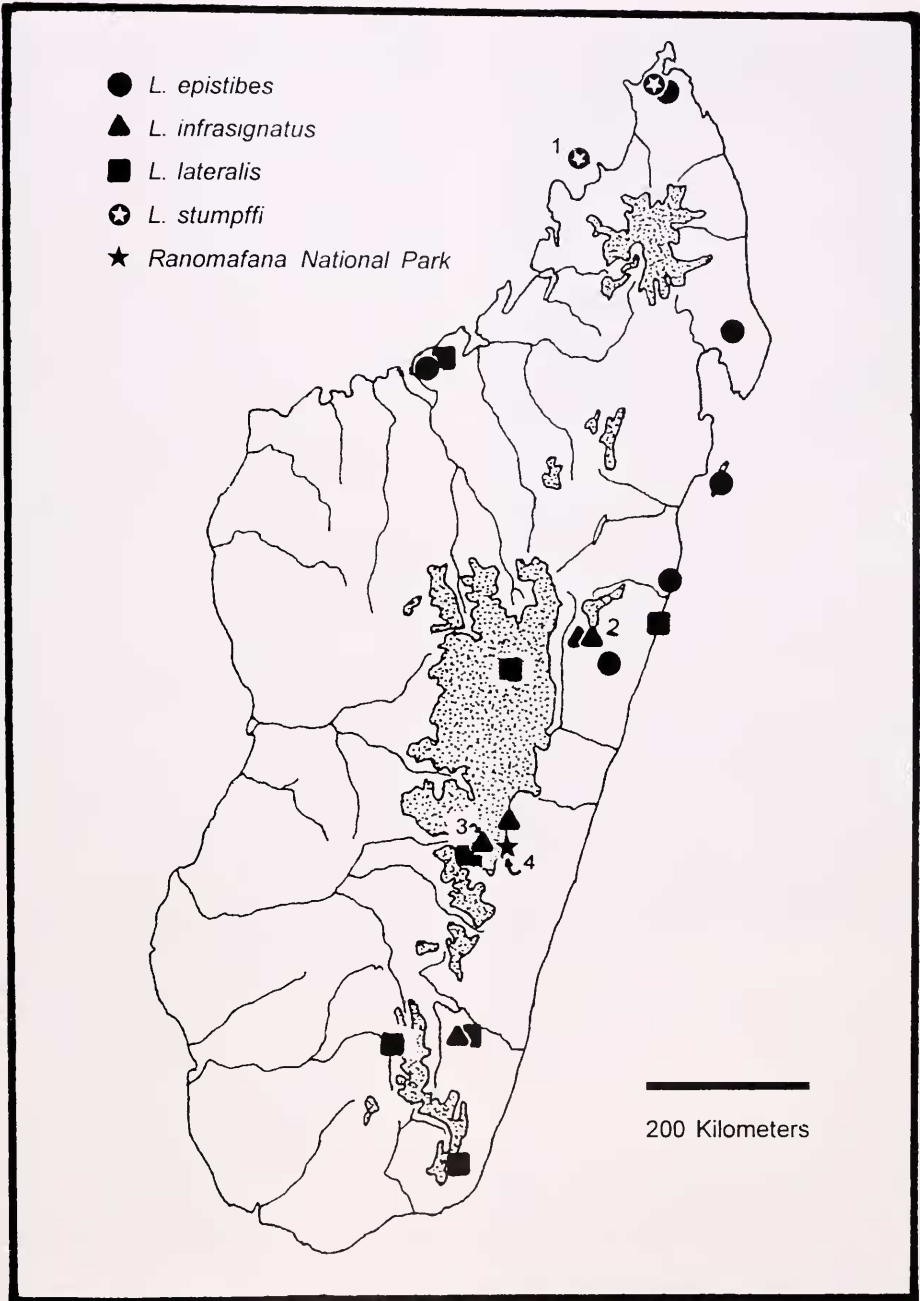


Figure 6. Localities for specimens examined of species of the *Liopholidophis stumpffi* group; these distributions are *not* comprehensive (see text for known distributions); shaded areas are above 1,000 m. All species indicated except *stumpffi* are known from the RNP, which is also the type locality for *epistibes*. Numbered localities referred to in the text and Appendix are (1) Nosy Be, type locality for *L. stumpffi* (Boettger); (2) Perinet [Andasibe], type locality for *L. thieli* Domergue [= *infrasignatus* (Günther)]; (3) Ankafana, type locality for *L. infrasignatus* (Günther); and (4) RNP.

The new species has 19 midbody scale rows and lacks extreme sexual dimorphism in tail length. Hence, it is a member of the *Liopholidophis stumpffi* group *sensu* Parker (1925) and is to be known as

*Liopholidophis epistibes*,  
new species

Figures 7–11

*Tropidonotus stumpffi* (not of Boettger, 1881a,b), part: Boulenger, 1893:247–248 (specimens f–g, h–i), 1915:374. Boettger, 1913:312 (specimen from Moramanga; identity inferred on basis of locality), 1913:322 (specimen from Nosy Sainte Marie, examined). Kaudern, 1922:445 (identity inferred on basis of locality; see “Distribution”).

*Liopholidophis stumpffi* (not of Boettger, 1881a, 1881b), part: Parker, 1925. Angel, 1936:127 (specimens from Tsianovoha; identity inferred on basis of locality). Domergue, 1973:1401; Glaw and Vences, 1994:338 (specimens from eastern Madagascar, as discussed later [see “Distribution”]).

? *Liopholidophis lateralis* (Duméril, Bibron, and Duméril), part: Guibé, 1954, 1958. See footnote 10.

**Holotype.** **Museum of Comparative Zoology (MCZ) 180322** (field number JEC 11460), an adult female in good condition (Fig. 7) from Talatakely, Ranomafana National Park, 950–1,000 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°16'S, 47°25'E]. Specimen obtained by John E. Cadle 20–26 December 1991.

**Paratypes.** The following specimens in the Museum of Comparative Zoology (MCZ) obtained by J. E. Cadle, identical locality data as for the holotype except the elevational range is 970–1,100 m: **MCZ 180312** (field number JE Cadle 9646), adult female, 24 October 1990; **MCZ 180313** (JEC 9802), adult female, 5 November 1990; **MCZ 180314** (JEC 9972), adult female, 24 November 1990; **MCZ 180315** (JEC 11078), adult female (skin + complete skeleton), 6–10 January 1992; **MCZ 180316** (JEC 11224), subadult male, 18 December 1991; **MCZ 180317** (JEC 11572), subadult female, 3 January 1992; **MCZ 180318** (JEC 11817), adult male, 7 December 1992; **MCZ 180319** (JEC 11836), adult male, 8 December 1992; **MCZ 180320** (JEC 11890), adult female, 11 De-

ember 1992; **MCZ 180321** (JEC 10609), adult female, 15 November 1990.

**MCZ 180323** (JEC 11427), adult female (fluid + skull), 27 December 1991, Trail between Ranovao and Menarano, approximately 3.5–5 km SSW (airline) Ranomafana, approximately 600 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°17'S, 47°28'E]. **MCZ 180324** (JEC 11797), adult female, 6–11 January 1992, Trail between Tsaratanana and Ambohipo, approximately 400–500 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°11'S, 47°37'E].

**SMF 57164**, adult female, Majunga, NW Madagascar, [Fivondronana Mahajanga: Mahajanga Province; 15°43'S, 46°19'E], 7 March 1960, K. L. Koch. **SMF 17579**, subadult female, St. Marie, E. Madagascar [=Nosy Sainte Marie], [Fivondronana Ambodifotatra, Toamasina Province; 16°50'S, 49°55'E], about 1905, A. Voeltzkow (see Boettger, 1913:322). **SMF 32526–28**, adult male and two subadult females, respectively, Col [colline (Fr.) = hill] Pierre Radama, Prov. Maroantsetra, [Fivondronana Maroantsetra, Toamasina Province; 15°17'S, 50°03'E] [part of H. Bluntschili collection, collected 1931; 1,000 m elevation *fade* Mertens, 1933; =Vozontanin-d Radama (“Radama Pass”) as listed by the Defense Mapping Agency, 1989].

**BMNH 89.8.1.8–9** (specimens f–g of Boulenger, 1893:247 [as *Tropidonotus stumpffi*]), adult males, Tamatave [=Toamasina], [Fivondronana Toamasina, Toamasina Province; 18°10'S, 49°23'E], M. Majastre. **BMNH 92.3.7.15–16** (specimens h–i of Boulenger, 1893:248 [as *Tropidonotus stumpffi*]), adult female and male (not individually tagged), Sahambendrana, Central Madagascar<sup>5</sup> [Toamasina Province; 19°24'S, 48°09'E], M. Majastre.

<sup>5</sup> Not located on recent maps or in gazetteers, Sahambendrana is a type locality for several anurans (e.g., *Mantidactylus tornieri* [Ahl, 1928]). Ahl (1928: 316–317) gives the locality as “Ankoraka Sahambendrana (Zentral-Madagaskar)” (“Anhoraka,” presumably as a misspelling, elsewhere). The coordinates given are for “Ankoraka” listed in the Defense Mapping Agency (1989) and correspond to this locality as used by Glaw and Vences (1994).



USNM 150593–94, adult female and subadult (probably female), respectively, Mt. d'Ambre [=Ambohitra; Fivondronana Antsiranana: Antsiranana Province; 12°30'S, 49°10'E], 1963, Howard E. Uible.

*Distribution.* Known from scattered localities on the eastern escarpment and lowlands, from at least the RNP in the southeast to the Masoala Peninsula in the northeast; Montagne d'Ambre and vicinity at the northern tip of Madagascar; the island of Nosy Sainte Marie off the east coast; and the vicinity of Mahajanga in northwestern Madagascar (Fig. 6). A record of "*stumpffi*" from Behara (24°57'S, 46°23'E) in extreme southeastern Madagascar (Domergue, 1973:1404; Glaw and Vences, 1994:336) may represent *epistibes*.

The distribution of *epistibes* in northern Madagascar and its distributional relationship with *stumpffi* are poorly understood. I suspect that all records for "*stumpffi*" given by Domergue (1973) and Glaw and Vences (1994), except for the island of Nossi-bé (type locality for *stumpffi*), actually represent *epistibes*; the same is probably true for records of "*stumpffi*" from Fandrarezana (16°45'S, 49°44'E) reported by Kaudern (1922:445), from Tsianovoha (=Tsianovoho; 21°57'S, 47°21'E) reported by Angel (1936:127), and from Moramanga (18°56'S, 48°12'E) reported by Boettger (1913:312). Nonetheless, specimens of "*stumpffi*" from northern Madagascar (e.g., Marojezy, as listed by Domergue, 1973, and Glaw and Vences, 1994) will have to be reexamined to determine whether or not they are referable to *epistibes*. For example, the specimen from Marojezy just mentioned (Domergue, 1973: table I) has an unusually high subcaudal count for *epistibes* females (102; cf. Table 2) but a rather typical one for *stumpffi* females; it may represent *stumpffi sensu stricto* (i.e., of Boettger, 1881a,b).

All specimens I examined from eastern Madagascar (Masoala Peninsula south) that would be referred to *Liopholidophis stumpffi sensu* Domergue (1973) and Glaw and Vences (1994) are referred to *epistibes*. I have seen specimens of *stumpffi*

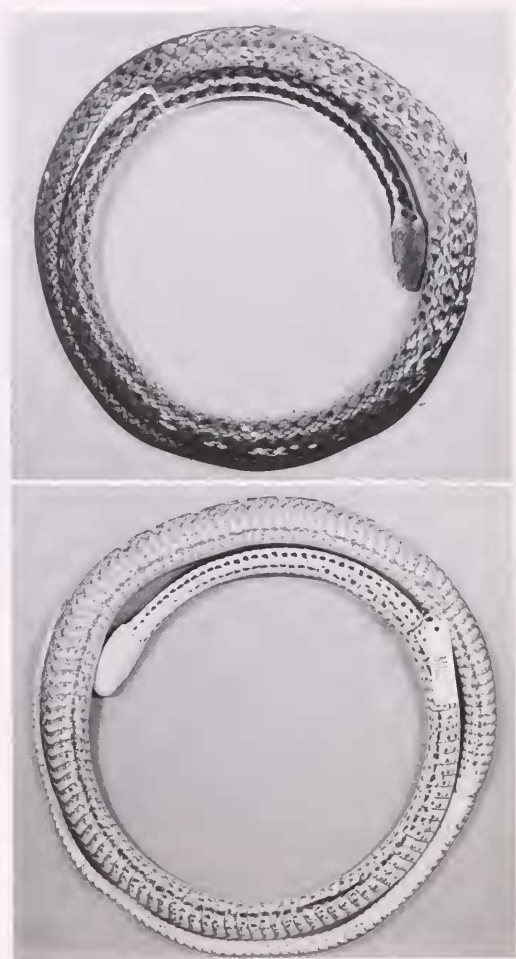


Figure 7. *Liopholidophis epistibes*, new species, holotype (MCZ 180322, female), in dorsal and ventral views. Approximately  $\times 0.46$ .

*sensu stricto* only from Montagne d'Ambre (Antsiranana) and vicinity in extreme northern Madagascar and from the island of Nosy Be (type locality; Fig. 6 and Appendix). It is unclear whether the populations of *epistibes* around Mahajanga and Montagne d'Ambre (Fig. 6) are isolated from the eastern part of the range or whether the distribution of *epistibes* is continuous throughout northern Madagascar.

Within the RNP, *Liopholidophis epistibes* is apparently widespread, with a

known elevational range of approximately 500–1,100 m. One confirmed locality, Tamatave (=Toamasina), is near sea level, assuming that Tamatave was not simply the shipping point.

*Etymology.* The specific epithet is an adjective meaning “on the trail,” modeled after the Greek ἀποστιβῆς (“off the path”; Liddell and Scott, 1968). From *epi* (“upon”) + *stibos* (“trail”), in reference to the usual circumstances in which I encountered this species.

*Diagnosis.* A species of *Liopholidophis* distinguished from all other species by the following combination of features: scales in 19 rows at midbody, reducing to 17 posteriorly; relatively long tail and high number of subcaudals (27–34% of total length and 86–104, respectively, sexes combined); dorsolateral light stripe on rows 5–7 or 5–6 on neck, 5–6 on anterior part of body, present or absent posteriorly (rows 4–5 when present); dark postocular stripe more or less continuous with series of dark blotches on side of neck, separating dorsolateral light stripe from light color of throat; anterior 10–30 ventral plates with series of black spots, usually elongate, inset 20–25% the width of the plate from lateral edge (venter otherwise may be more or less immaculate, but usually heavily spotted and/or suffused with black or dark gray, especially posteriorly).

*Liopholidophis epistibes* differs from members of the *sexlineatus* group in having 19–19–17 dorsal scale rows (vs. 17–17–15). It differs from other members of the *stumpffi* group, *stumpffi*, *lateralis*, and *infrassignatus*, primarily in aspects of color pattern.

*Liopholidophis epistibes* and *L. stumpffi* are separable by the disposition of the dorsolateral light stripes and other pattern characteristics (see “Remarks” for more detailed comparison of specimens of both species from the region of sympatry). In *epistibes*, the light stripe occupies scale rows 5–6 or 5–7 anteriorly, 5–6 at midbody and, when present posteriorly, rows 4–5; the stripes are not continuous with the light color of the throat (separated by conflu-

ence of postocular dark stripe and dark pigment on lateral surface of neck; Fig. 8). In *stumpffi*, the dorsolateral stripe occupies rows 4–5 anteriorly and at midbody (posteriorly indistinct in adults I have seen, but appears to be restricted to row 4; see “Remarks” in species account for *stumpffi*); it is confluent with the light coloration of the throat (Fig. 8). The dark postocular stripe is comparatively broad in *epistibes*, is confluent with dark blotches on the side of the neck (occasionally briefly interrupted), and occupies the middle to lower half of the ultimate supralabial (Fig. 8); the postocular stripe in *stumpffi* is narrower, occupies the upper portion and/or suture line of the ultimate and penultimate supralabials, and does not continue posterior to the jaw angle (Fig. 8). The dark head cap does not extend well below the jaw line in *epistibes*, whereas in *stumpffi* the dark head cap curves around the angle of the jaw (Fig. 8). The two species also differ in ventral pattern (cf. Figs. 7, 11, and 24): virtually immaculate in *stumpffi* except for encroachment of dark flank pigment laterally, and usually a series of indistinct punctations at extreme anterolateral edge of ventral plates (not inset from edge); usually heavily spotted or suffused with dark gray or black in *epistibes*, especially posteriorly, and with series of discrete, elongate black spots on each side of anterior 10–30 ventral plates, inset 20–25% from the lateral edges of the plates (Fig. 8). *Liopholidophis epistibes* averages about 10 more ventral plates in both sexes than *stumpffi*, and the ranges in the two species are virtually nonoverlapping (Table 2). Hemipenes of *epistibes* and *stumpffi* (described in detail later) also differ: *epistibes* has about three rows of enlarged spines on the outer surface at the base of each hemipenial lobe, whereas *stumpffi* has only a single row; in addition, nude areas between the lobes are more extensive in *epistibes* than in *stumpffi*.

*Liopholidophis epistibes* differs from *L. lateralis* in the position of the lateral stripes: in *epistibes* on dorsal rows 5–6 or 5–7 anteriorly, 5–6 at midbody, usually fading

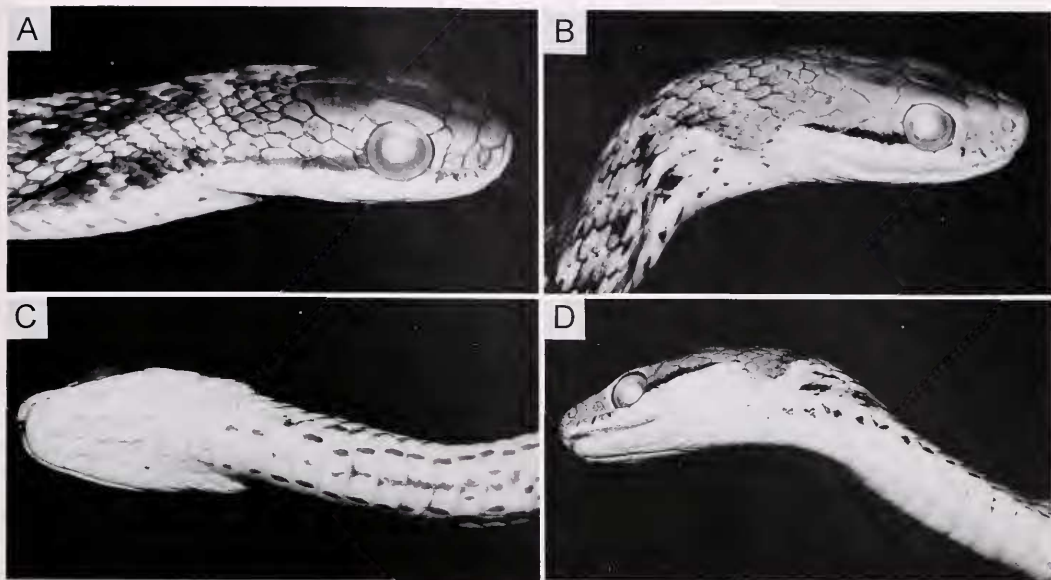


Figure 8. Comparison of *Liopholidophis epistibes*, new species (A, C; MCZ 180319), and *Liopholidophis stumpffi* (Boettger) (B, D; SMF 17577), showing the following distinguishing features of head and neck. (1) Postocular bar extending diagonally across ultimate supralabial, intersecting lower edge of ultimate supralabial at the mouth line (*epistibes*); restricted to upper edge and suture line of ultimate supralabial (*stumpffi*). (2) Postocular bar confluent with black pigment on side of neck (*epistibes*); postocular bar short, ending on last supralabial (*stumpffi*). (3) Dorsolateral light stripe separated from light gular coloration by confluence of postocular bar and black spots on side of neck (*epistibes*); continuous with light coloration of gular region (*stumpffi*). (4) No dark wedge from head cap extending below mouth line at angle of jaw (*epistibes*); dark wedge from head cap extends below mouth line (*stumpffi*). (5) Discrete, elongate dark spots laterally on anterior ventrals, but inset from lateral edge of ventral plates (*epistibes*); spots, when present, diffuse, rounded, and present at extreme anterolateral edges of ventral plates (*stumpffi*).

posteriorly (and nearly always indistinct on tail); and anteriorly separated from the light color of the throat by dark pigment on the side of the neck (Figs. 8, 23). In *lateralis*, the lateral stripes are centered on row 4, with adjacent rows usually involved; the stripes are distinct the length of the body, continue to the tail tip, and are continuous with the light color of the throat (occasionally barely separated by a narrow extension of the dark flank color; Figs. 23, 26; see also Glaw and Vences, 1994:fig. 505). The venter of *epistibes* may or may not be generally speckled with black (Figs. 7, 11), whereas that of *lateralis* never appears to be (black spots sometimes present at lateral edges of ventral plates).

*Liopholidophis epistibes* has a longer tail (27–34% of total length, sexes combined) and more subcaudals (91–104, males; 86–96, females) than *infrasignatus* (tail 21–

27%; subcaudals 66–81, males; 62–73, females) (see Table 2, including footnote 1 for possible amplification of ranges for *epistibes*). *Liopholidophis epistibes* is also of more gracile habitus than *infrasignatus*, and the anterior dorsal colors are predominantly contrasting black and yellow (browns, olive browns, to olive gray in *infrasignatus*). The orientation of the postocular dark bar also differs somewhat in *epistibes* and *infrasignatus*. In *epistibes*, the bar extends more or less horizontally posterior to the eye, passing across the upper portion of the penultimate supralabial (Figs. 8, 23); in *infrasignatus*, the bar extends at an angle downward across the penultimate supralabial, usually having a somewhat separated portion on the lower portion of the ultimate supralabial (Figs. 23, 28).

*Data on the Holotype* (MCZ 180322).

The holotype is a gravid adult female with five eggs, as determined by palpation. Total length 753 mm; tail length 218 mm (29% of total length). Greatest head width (parietal region) 9.75 mm, head length 18.95 mm from tip of snout to end of mandibles. Horizontal diameter of eye 3.91 mm; anterior edge of eye to posterior edge of nostril 2.87 mm. Dorsals 19-19-17, the reduction occurring by fusion of rows 3 + 4 at the level of ventral 108. Three pre-ventrals, 166 ventrals, divided anal plate, 90 pairs of subcaudals. 8-8 supralabials (4-5 touching eye), 10-10 infralabials, 2 + 2 temporals on each side, 26 + 2 right maxillary teeth with essentially no diastema. Weight in life 44 g.

*Description.* The following description is based on the 16 females and 8 males in the type series. Measurements, proportions, and scutellation are summarized in Table 2 (see footnote 1 in Table 2 for possible extreme values for some statistics reported here). Largest specimen a female, 829+ mm total length, tail 195+ mm; largest male 709 mm total length, 238 mm tail length. Tail length not sexually dimorphic, 28-34% of total length in males, 27-31% in females. Dorsal scales smooth, in 19-19-17 rows; 0-2 apical pits present (see "Remarks"). Scale row reduction from 19 to 17 rows by fusion of rows 3 + 4 (occasionally appearing as loss of either row 4 or 3) at the level of ventrals 87-108 (N = 12). Ventrals 157-166 in males, 151-167 in females. Anal plate divided. Subcaudals 91-104 in males, 83-96 in females. Eight upper labials (rarely seven or nine) with 4-5 touching eye. Lower labials usually 10-10 (14 specimens), with 8-8 (1), 9-10 (5), 10-11 (1), or 11-11 (1) being uncommon variants; first pair in contact behind the mental, 1-4 or 1-5 touching an anterior genial, 4-5 or 5-6 touching a posterior genial. Anterior genials shorter than posterior genials. Loreal present. Preocular single. Temporals usually 2 + 2 (rarely 1 anterior or posterior temporal; in one instance, 3 posterior temporals).

Body form slender (Figs. 9-10), slightly higher than wide; ventrolateral edge of

body slightly angulate to rounded. Head slightly wider than neck. Pupil round. Eye large (Figs. 8, 23), its diameter greater than the distance between eye and posterior edge of nostril ( $\bar{x} = 1.36 \pm 0.18$ ; range 1.10-1.69; N = 13). Scattered pits and tubercles present on head plates.

Hypapophyses (MCZ 180315, complete skeleton) on posterior trunk vertebrae keellike, with a low projecting vane, and a bluntly pointed posterior projection extending beneath the centrum of the next posterior vertebra.

*Dentition.* Maxillary teeth 22-29 + 2 (N = 16;  $\bar{x} = 26.4 \pm 2.06$  prefang teeth). Diastema absent; gap < 1 tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row, 2 times as large as the posteriormost maxillary teeth; having a rounded anterior surface (except for distal portion, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed. Two skulls (MCZ 180315 and 180323, both females) have the following numbers of teeth, respectively: 17-20, 19-17 palatine teeth; 34-36, 37-38 pterygoid teeth; and 31-30, 32-31 dentary teeth.

Domergue (1973) reported 16-17 prefang maxillary teeth in *Liopholidophis epistibes* ("*stumpffi*"), which, in comparison to my counts, suggests failure to count empty sockets or otherwise erroneously low counts. Nevertheless, the range of maxillary tooth counts in my series is broad. Any geographic pattern is, however, difficult to discern because most of my counts are from the RNP series, where the range is 24-29 prefang teeth.

*Hemipenis* (see Fig. 34). Deeply bilobed, noncapitate, acalyculate (ornamentation consists entirely of spines), with a very short basal stalk. Sulcus spermaticus deeply bifurcate, centrolineal. The lobes diverge strongly from one another, lying at essentially right angles to the stalk. Tips of lobes with a central depression ("umbelliform", as described later [see "Hemipenial Morphology in *Liopholidophis*"]).

*Coloration in Life* (see Glaw and



Figure 9. *Liopholidophis epistibes*, new species. Specimen from the RNP, MCZ 180319, showing typical fading of dorsolateral stripes about midbody.



Figure 10. *Liopholidophis epistibes*, new species. Specimen from the RNP, MCZ 180323. This specimen has unusually complete and vivid dorsolateral stripes, extending not only the length of the body, but the tail as well.

Vences, 1994:pl. 347 of "stumpffi"). MCZ 180312 (female)—Dorsum greenish brown anteriorly, grading to rich medium brown by midbody, to olive brown posteriorly. Yellow dorsolateral stripes begin on nape, turning to yellowish brown but becoming indistinct by midbody. Top of head olive greenish. Black postorbital stripe extending across middle portion of posterior supralabial, and continuous with lateral stripe or series of blotches on side of neck. Upper labials, lower labials, and throat pale yellow. Venter olive greenish with black speckling laterally.

MCZ 180313 (female)—Anteriorly, middorsum and flanks black, gradually fading to dark olive brown by  $\frac{1}{3}$  of the way along the body. Posterior dorsum dark olive brown with vague obscure black spotting and flecks. Dorsolateral pale yellow stripe begins on nape and rapidly fades to yellowish brown, widening and fading posteriorly so that it is barely distinct from middorsal and lateral areas. Top of tail dark brown. Top of head olive brown. Pupil round. Iris dark brown. Black postocular stripe extends diagonally across the middle of the ultimate supralabial to angle of jaw. Upper labials anterior to eye olive; posterior ones pale yellow. Lower labials and gular region pale yellow. Anteriorly, ventrals and first scale row pale yellow; black spot inset from lateral edge of ventrals. All ventrals posterior to approximately the first 10 heavily flecked and spotted with black. Ventral ground color pale yellow anteriorly, fading to brownish yellow, with orangish wash on posterior  $\frac{2}{3}$  of body. Subcaudals dirty white with very light orange tinge, unmarked except for a few scattered black specks.

The color plate of *Liopholidophis "stumpffi"* given by Glaw and Vences (1994:pl. 347; specimen from Perinet [=Andasibe]) is of *L. epistibes*. That specimen is similar to coloration of some specimens from the RNP, but the dorsolateral stripes in RNP specimens tend to be more intensely yellow. Most specimens have a paired series of discrete black blotches (usually slightly offset) between the dor-

solateral stripes on the neck and anterior body and a series along the flanks below the dorsolateral stripes in the same area. Blotches in the lateral series are large (4–7 scales in diameter), squarish, connected anteriorly with the postocular stripe, and sometimes more or less fused with one another. Both the dorsal and lateral blotches become smaller posteriorly, either remaining as small punctations the length of the body or disappearing altogether.

*Coloration in Preservative.* Freshly preserved specimens retain much of the original pattern, although the dorsal ground colors become brown to olive brown (blackish anteriorly), and the dorsolateral stripes become greenish yellow, fading to light grayish posteriorly. The stratum corneum is lost easily from the dorsal scales, giving such specimens a grayish cast. The venter becomes dirty yellowish or whitish, with dark gray or black markings. The amount of black pigment on the venter varies considerably in the RNP sample—from almost none to heavy spotting or general suffusion with dark pigment, most prominent posteriorly (Figs. 7, 11).

Consistent features of the pattern in *Liopholidophis epistibes* include the dorsolateral light stripe involving scale rows 5–6 or 5–7 anteriorly, separated from the light gular coloration by extension of the dark postocular stripe along the neck (Figs. 8, 23). The dorsolateral stripes usually broaden on the nape (Figs. 7, 10), giving the appearance of a pair of light nape spots connected to the stripes. Otherwise, the dorsolateral stripes vary considerably in length and discreteness; in most specimens they fade (but are still evident) by midbody (Fig. 9), but in others they are discrete well onto the tail (Fig. 10). In most specimens, scattered dorsal scales on the anterior body have bright white borders. The lower portion of scale row 1 is lighter (yellowish in life) than the other dorsal rows. A series of discrete, elongate black spots on the anterior 10–30 ventral plates, and inset 20–25% from the lateral edge of the plate, is a constant feature (Fig. 8). Otherwise, the venter is highly variable in

pattern: more or less immaculate (Fig. 11), having an additional median series of spots or continuous line that may run the length of the body (Fig. 7), having irregular dark splotches of varying densities (Fig. 11), being generally suffused with dark pigment and spotting, or some combination of the preceding. Ventral pigmentation is nearly always denser posteriorly than anteriorly. The ventral pigmentation does not seem to develop ontogenetically, as some small juveniles (e.g., MCZ 180316; SVL 197 mm) already show extensive development of posterior spotting on the venter (as well as the anterior ventral spots characteristic of *epistibes*).

**Natural History.** *Liopholidophis epistibes* is diurnal and terrestrial. Most specimens from the RNP were collected actively crossing trails during morning hours, occasionally sunning in leaf litter or bare earth on trails. Most specimens were collected from primary montane rainforest, 950–1,100 m elevation; two specimens were from degraded secondary growth at lower elevations in the RNP area.

*Liopholidophis epistibes* dorsoventrally flattens the neck in defensive display, highlighting the white borders to some of the dorsal scales and exposing white patches of skin between; it bites readily. The white patches of skin are generally adjacent to scales with white borders; otherwise, the skin is dark grayish, enhancing the effect of the white patches when the neck is inflated.

Two specimens of *Liopholidophis epistibes* contained food. MCZ 180319 (SVL 421 mm) contained one *Platypelis pollicaris*, a small, nocturnal, arboreal microhylid frog, swallowed head first. MCZ 180318 (SVL 390) contained one *Plethodontohyla alluaudi*, a small terrestrial (leaf-litter) microhylid, swallowed head first.

Three females from the RNP contained eggs: MCZ 180313 (SVL 522 mm; collected 5 November; 6 unshelled oviductal eggs), MCZ 180314 (SVL 558 mm; 24 November; 6 unshelled oviductal eggs), and MCZ 180322 (SVL 535 mm; 20–26 December; 5 shelled oviductal eggs). No em-

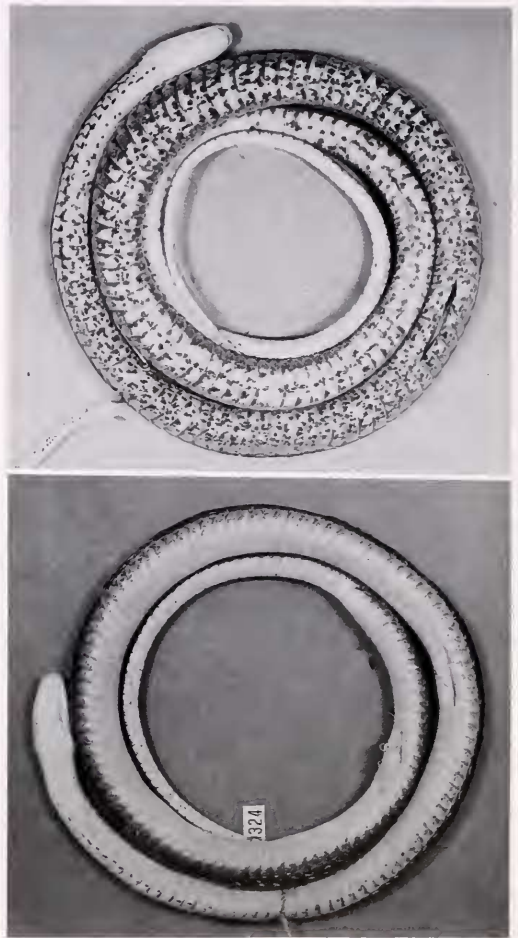


Figure 11. Variation in ventral pigmentation in *Liopholidophis epistibes* from the RNP. Top: MCZ 180313. Bottom: MCZ 180324. The latter specimen had the least ventral pigmentation of any specimen of *epistibes* examined, but even so still had the elongate spots on anterior ventrals. See also Figure 7.

bryos were detected in the first two; MCZ 180322 (holotype) was not dissected. Domergue (1973) reported gravid females of *Liopholidophis epistibes* (“*stumpffi*”) (SVLs 605–675 mm; all from Perinet) containing 3–6 eggs in November and December, and a female (SVL 567 mm) from Perinet that laid a clutch of 4 eggs (2 additional eggs unpassed) on 19 December. Thus, *Liopholidophis epistibes* is oviparous.

In the RNP area, *Liopholidophis epis-*

*tibes* is microsympatric with the following species of the genus: *rhadinæa*, *infrasignatus*, *dolicocercus*, and *lateralis*—and more broadly sympatric with *grandidieri* and *sexlineatus*. *Liopholidophis epistibes* is broadly sympatric with *L. stumpffi* in the vicinity of Montagne d'Ambre in northern Madagascar (see "Remarks").

*Remarks.* From the region of broad sympatry between *epistibes* and *stumpffi* in the vicinity of Montagne d'Ambre (=Antsiranana; Fig. 6), I examined two specimens of *epistibes* (USNM 150593–94, adult female and small juvenile, probably female, respectively) and three specimens of *stumpffi* (MCZ 54368, adult female; MNHN 1893-211, adult male; and USNM 150595, small juvenile male). All of these specimens are readily identified by characters given in the diagnosis, with no intermediacy apparent.

The two specimens of *epistibes* from the Montagne d'Ambre area are somewhat distinguishable from the other specimens of *epistibes* examined in the following ways that may indicate geographic variation: (1) their ventral counts (151–152) are lower than the range for other specimens (157–167) (a trend weakly suggested by their low subcaudal counts as well), and (2) the black spots on the anterior ventrals are less elongate, somewhat smaller, and more irregular than those of other specimens. Nonetheless, the ventral spotting is typical of *epistibes*, and none of the specimens of *stumpffi* showed any approach to this type of patterning. USNM 150593 (adult female) has extensive irregular spotting on the posterior venter, as is characteristic of many specimens of *epistibes*, but unknown in *stumpffi*.

Domergue (1973) reported apical pits as lacking in *Liopholidophis epistibes* ("*stumpffi*"), with the exception of one specimen having two apical pits. My observations revealed that the number of apical pits varies from 0 to 2 within an individual, often with only widely scattered dorsal scales having pits. Some individuals had much greater frequency of pits than others; when present, the pits seemed to

be more frequent on midbody and posterior dorsal scales than on the anterior scales.

The Malagasy name *tsiririatra* is used in the RNP region for *Liopholidophis epistibes*, similar to the name *antsiririatra* reported by Domergue (1973:1405) for this species in east central Madagascar.

#### SYNOPSIS OF OTHER SPECIES OF LIOPHOLIDOPHIS

##### *Liopholidophis* Mocquard, 1904

*Type Species.* *Liopholidophis grandidieri* Mocquard, 1904 (designated by Williams and Wallach, 1989:87).

*Content.* Nine recognized species, as follows: *Liopholidophis dolicocercus* (Perracca), *Liopholidophis epistibes* Cadle, *Liopholidophis grandidieri* Mocquard, *Liopholidophis infrasignatus* (Günther), *Liopholidophis lateralis* (Duméril, Bibron, and Duméril), *Liopholidophis pinguis* Parker, *Liopholidophis rhadinæa* Cadle, *Liopholidophis sexlineatus* (Günther), *Liopholidophis stumpffi* (Boettger). One undescribed species is recorded from Montagne d'Ambre at the northern tip of Madagascar (Raxworthy and Nussbaum, 1994a), from where *stumpffi* and *epistibes* are also known (see later).

*Distribution.* Madagascar.

#### KEY TO SPECIES

Most species of *Liopholidophis* can be distinguished by details of color pattern, tail proportions, and certain scale characters (especially dorsal scale rows and subcaudal counts). With the possible exception of separating *sexlineatus* and *pinguis* in the last couplet, the following key should allow easy identification of specimens. Males of *sexlineatus* and *pinguis* are easily separated on the basis of relative tail lengths and subcaudal counts, but females are not (and males of the latter, lacking extremely elongate tails, are easily mistaken for females of the former); previous keys (Parker, 1925; Guibé, 1958; Glaw and Vences, 1994) reliably identify only males. Compounding the difficulty is the fact that



I have seen only 11, mostly rather old, specimens of *pinguis*, and the extent of variation in mensural and meristic characters is unknown in that species; in any case, the variation in such features overlaps considerably when females of *sexlineatus* and *pinguis* are compared (cf. Table 1). Parker (1925) commented that *pinguis* was "of rather stouter habit than its allies" (*pinguis* [L.] = fat), but that seems clearly true only when comparing larger specimens of *pinguis* to such rather gracile species as *rhadinaea* and *stumpffi* (Parker had only a single specimen of *pinguis*, and that specimen is exceptionally large, perhaps giving a misleading impression of body form). Similarly, the head plate proportions used by Parker (1925:key) to characterize *pinguis* would not likely stand rigorous scrutiny with additional specimens and statistical comparisons. The pattern characters used in the following key appear to work well for the specimens examined (see also "Species Accounts"), but users of the key should be aware that the characteristics used in couplet 8 may not hold once *pinguis* is better understood. Much variation also exists in pattern and scalation in the nominal taxa *lateralis* and *sexlineatus*, and these taxa may be found to be composites once that variation is more thoroughly studied.

Following the key, the species accounts treat the five species of *Liopholidophis* in addition to *rhadinaea* and *epistibes* occurring within the RNP and, in addition, provide brief notes on *pinguis* and *stumpffi*.

- 1. Dorsal scales in 19 rows at midbody, reducing to 17 posteriorly ..... 2
- Dorsal scales in 17 rows at midbody, reducing to 15 ..... 5
- 2. Dorsal ground color black to grayish black; light dorsolateral stripe centered on row 4 (with parts of adjacent rows also involved), continuous and vivid from neck to tail tip, anteriorly confluent with light color of throat; venter usually immaculate except for spots at extreme lateral edges of ventrals in some specimens .....  
     ..... *Liopholidophis lateralis* (Duméril, Bibron, and Duméril)
- Dorsal ground color brown, olive, or blackish

- (may be grayish in preservative); light dorsolateral stripe anteriorly on rows 4-5, 5-6, or 5-7 (often indistinct on posterior body and tail, but usually on rows 4 or 4-5 posteriorly when present); dorsolateral stripe anteriorly confluent or not with light color of throat; venter often heavily marked with blackish pigment, which may tend to form midventral line ..... 3
- 3. Tail short: 23-27% of total length in males, 21-24% of total length in females; fewer than 85 subcaudals in males, fewer than 75 in females; venter with or without dark pigment, which may tend to form broken longitudinal lines; dorsolateral light stripe anteriorly on rows 5-6 .....  
     ..... *Liopholidophis infrasignatus* (Günther)
- Tail rather long: 28-34% of total length in males, 27-34% of total length in females; more than 90 subcaudals in males, more than 80 in females; venter with or without dark pigment; dorsolateral light stripe anteriorly on rows 5-6, 5-7, or 4-5 ..... 4
- 4. Dorsolateral light stripe anteriorly on scale rows 5-6 or 5-7, separated from light color of throat by dark pigment; black postocular stripe extending diagonally across middle or lower portion of posteriormost supralabial, and continuous with black pigment on side of neck; venter immaculate or (usually) with dark spots or general dark suffusion, especially posteriorly; anterior ventrals with elongate black spots inset 20-25% from edges of plates; dark wedge of head cap does not extend ventral to mouth line at jaw angle ..... *Liopholidophis epistibes* Cadle
- Dorsolateral light stripe anteriorly on scale rows 4-5, continuous with light throat pigment behind angle of jaws; black postocular stripe on posteriormost supralabial restricted to uppermost part of scale and/or dorsal suture line, ending at posterior supralabial (not continuous with dark lateral neck pigment); venter essentially immaculate except for dark dorsal pigment narrowly encroaching laterally; dark spots on anterior ventrals, when present, at extreme lateral edges of plates; dark head cap extends as a wedge ventral to mouth line at jaw angle ..... *Liopholidophis stumpffi* (Boettger)
- 5. Ventral scutes (except for anteriormost) solid black, or black with regular creamy white border (forming cream stripe at lateral edge of ventral plates). Dorsum uniform brownish; with black reticulations, blotches, or chevrons (especially posteriorly); or with general black suffusion. Lateral or ventrolateral black stripe may be present on rows 2 + 3, and/or row 1 + adjacent edge of ventrals ..... 6
- Ventral scutes never solid black, or black with bordering cream-colored stripe (may be im-

- maculate to heavily, but irregularly, spotted or patterned with dark pigment). Dorsum distinctly striped or not (when present, consisting of dark and light brown stripes, or lateral black stripes); never with dark reticulations, paired blotches, or chevrons
6. Venter solid black (no white or cream stripe at lateral edge of ventral scutes); lateral black stripe on rows 2 + 3; subcaudals more than 200 in males, more than 100 in females . . . . . *Liopholidophis grandidieri* Mocquard
- Venter black with cream or white stripe at lateral edges of ventral scutes; black stripe at juncture of ventral plates and first dorsal row, but no lateral black stripe on rows 2 + 3; subcaudals less than 200 in males (highest observed, 164), less than 100 in females (highest observed, 88) . . . . . *Liopholidophis doliocercus* (Peracca)
7. Size diminutive and slender (maximum <750 mm total length in males, <500 mm in females); 3 light (yellowish in life) nape spots; striped pattern consisting of contrasting shades of brown with broad median dorsal dark brown stripe 3–5 scales wide, bordered by narrow light yellowish brown stripe centered on row 6; venter pink to red in life, unmarked except for occasional fine dark peppering . . . *Liopholidophis rhadinaea* Cadle
- Size larger and more robust (maximum >850 mm total in males, >650 mm in females); no light nape spots; dorsal pattern striped or not, but stripes black when present; venter not pink to red in life, often densely marked with dark pigment . . . . . 8
8. Relative tail length not strongly sexually dimorphic (in males 30–35% of total length, in females approximately 25% of total); subcaudals in males <110; stripes usually indistinct at least on anterior part of body, more distinct on posterior body and tail (when present, consisting of blackened suture line between ventrals and dorsal row 1, and lateral stripe or series of spots or dashes on row 3 anteriorly, dropping to suture line between 2 and 3 posteriorly; venter not heavily marked with black (some specimens with edges of ventrals marked with black, or with lateral or median series of small spots) . . . *Liopholidophis pinguis* Parker
- Relative tail length strongly sexually dimorphic (in males >40% of total length, in females 24–30%); subcaudals in males >120; stripes distinct entire length of body and tail (consisting of black stripe at border between ventrals and dorsal row 1, and lateral stripe involving rows 2 + 3, occasionally 4; indistinct stripe sometimes present at the suture between rows 6 and 7; occasionally rows 1–3 and adjacent venter are entirely black); venter more or less immaculate, to

heavily and irregularly marked with black . . . . . *Liopholidophis sexlineatus* (Günther)

The *sexlineatus* Species Group (Parker, 1925)  
 Figures 12–22 (see also Figs. 1–2, 4–5);  
 Table 1

**Content.** *Dromicus sexlineatus* Günther, 1882:264.  
*Dromicus doliocercus* Peracca, 1892:1–3.  
*Liopholidophis grandidieri* Mocquard, 1904:304.  
*Liopholidophis pinguis* Parker, 1925:390.  
*Liopholidophis rhadinaea* Cadle, present work.

*Liopholidophis doliocercus*  
 (Peracca)  
 Figures 12–17

*Dromicus doliocercus* Peracca, 1892:1–3, fig. 1a–d (Type locality, “Valle dell’Umbi (Andrangoloka)” [Valley of the Umbi River (Andrangoloka)] [=Andrangoloka]. Holotype, Museo Regionale di Scienze Naturali, Torino (MZUT) 796 (Fig. 13). Peracca (1892:3) was explicit about basing his specific epithet on the Greek word δόλιχος but incorrectly transliterated the name as *dolicos*, rather than correctly as *dolichos*. Under Article 32b-c of the *International Code*, however, his name stands as the correct original spelling, despite having been unjustifiably emended by all subsequent authors except Parker (1925). The name is here resurrected from the synonymy of *Liopholidophis sexlineatus* (e.g., Guibé, 1958; see “Remarks”).

*Liopholidophis dolichoercus* [unjustified emendation] (Peracca): Mocquard, 1904:302, 1909:43, 97; Werner, 1929:11. (Elsewhere in Mocquard’s 1904 paper, the incorrect spelling *dolischocercus* is found.)

*Tropidonotus dolichoercus* [sic] (Peracca): Boettger, 1898:25, 1913:312; Boulenger, 1893:246, 1896:607, 1915:373. Boulenger’s (1893, 1896) listing of two females in the British Museum under this name are based on misidentified specimens of the then-undescribed and very similar species *Liopholidophis grandidieri* Mocquard (1904) (these specimens are discussed under the species account for *grandidieri*, later). Boulenger listed both *dolichoercus* [sic] and *grandidieri* in the 1915 paper, but his concept of the former seems to have been based on the same misidentified specimens he had cited earlier.

*Liopholidophis doliocercus* (Peracca): Parker, 1925:392.

*Liopholidophis sexlineatus* (Günther), part: Guibé, 1958:216; Brygoo, 1983:39 (footnote 29) (*Dromicus dolichoercus* [sic] Peracca listed as synonym).

**Holotype** (Fig. 13). Museo Regionale di Scienze Naturali, Torino (MZUT) 796, a male in fair condition (probably subadult based on size), 427 mm total length, 162

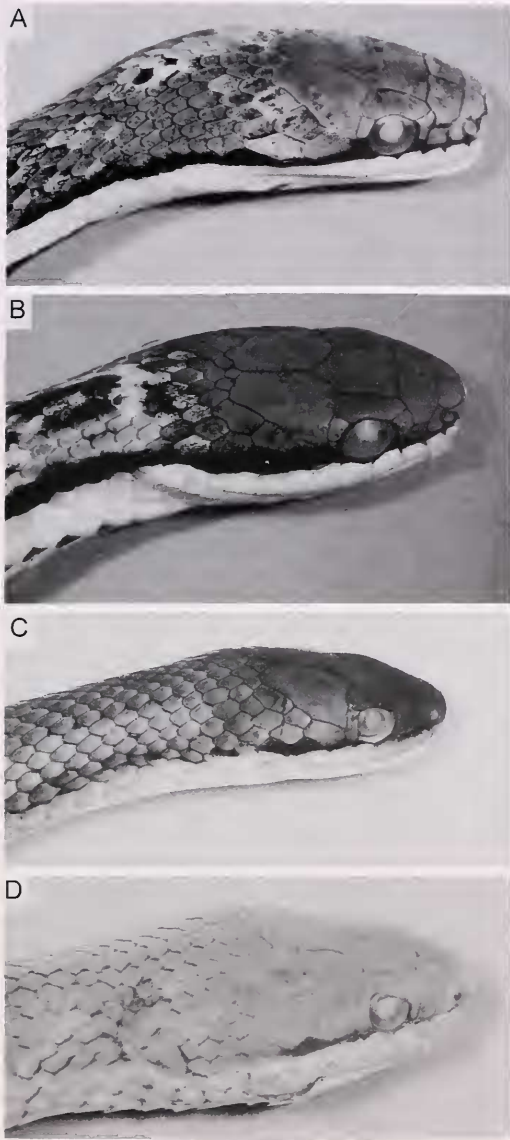


Figure 12. Heads of four species of the *Liopholidophis sexlineatus* group, in dorsolateral view (see also Figs. 2 and 19 for *L. rhadinaea* and *L. grandidieri*, respectively). A. *L. doliocercus* (Peracca) (MCZ 180405). B. *L. grandidieri* Mocquard (BMNH 95.7.4.32). C. *L. sexlineatus* (Günther) (MCZ 180331). D. *L. pinguis* Parker (USNM 149242).

mm tail length (38% of total length), with 160 ventrals and 164 subcaudals (Peracca, 1892; see "Remarks" concerning subcaudals). I examined color transparencies of the type, including details of head and

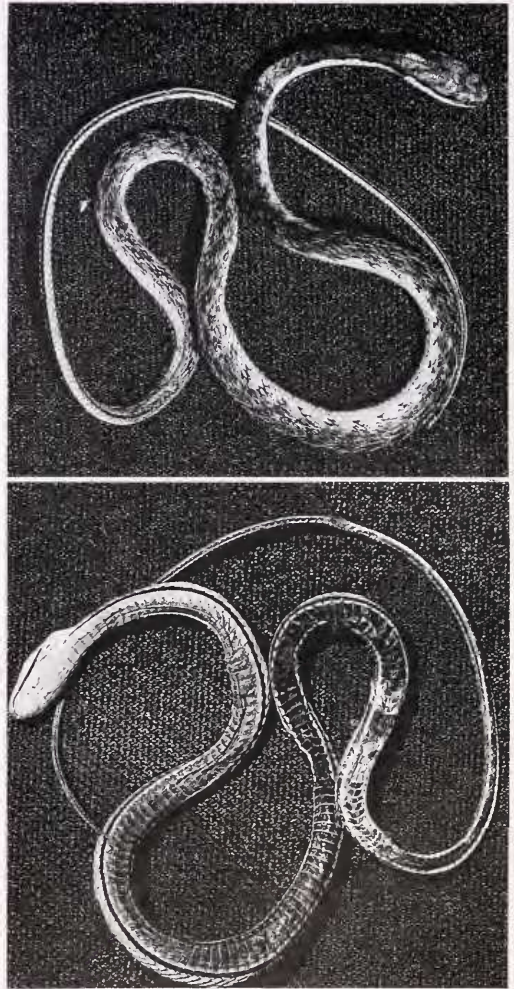


Figure 13. *Liopholidophis doliocercus* (Peracca), dorsal and ventral views of the male holotype (MZUT 796). Photographs by Dr. Franco Andreone.

body. Peracca's (1892) description of the type is excellent.

**Diagnosis.** A species of *Liopholidophis* having 17–17–15 dorsal scale rows; tail 39–44% total length and 140–164 subcaudals in males; and a black venter with a marginal white stripe, a black stripe at the suture between the ventral plates and dorsal row 1, but no lateral stripe involving rows 2–3.

*Liopholidophis doliocercus* differs from *sexlineatus*, where it has been synony-

TABLE 1. VARIATION IN MENSURAL AND MERISTIC CHARACTERISTICS OF SPECIES OF THE *LIOPHOLIDOPHIS* *SEXLINEATUS* GROUP. SCALE COUNTS AND BODY PROPORTIONS ARE  $\bar{x} \pm SD$  (SAMPLE SIZE) WITH RANGES BELOW IN PARENTHESES; MAXILLARY TOOTH COUNTS ARE PREFRANG COUNT RANGES (+2 FANGS), FOLLOWED BY  $\bar{x} \pm SD$  (SAMPLE SIZE). TABULATIONS FOR *DOLICOCERCUS* AND *PINGUIS* INCLUDE DATA ON THE HOLOTYPE FROM PERACCA (1892) AND PARKER (1925), RESPECTIVELY.

	<i>rhadimaea</i>	<i>dolicocercus</i>	<i>grandidieri</i>	<i>sexlineatus</i>	<i>pinguis</i>
	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15
Dorsals					
Ventrals					
Males	174.4 $\pm$ 3.64 (7) (170-179)	156.2 $\pm$ 2.86 (5) (152-160)	170.0 $\pm$ 1.41 (2) (169-171)	153.4 $\pm$ 4.01 (15) (147-163)	150.8 $\pm$ 2.93 (6) (147-154)
Females	156.3 $\pm$ 2.77 (11) (150-160)	146.0 $\pm$ 3.16 (4) (143-150)	154.0 $\pm$ 9.9 (2) (147-161)	145.1 $\pm$ 2.02 (14) (141-148)	142.4 $\pm$ 3.43 (5) (139-147)
Subcaudals					
Males	130.67 $\pm$ 4.72 (6) (126-137)	155.2 $\pm$ 10.47 (5) (140-164)	218.0 $\pm$ 4.24 (2) (215-221)	150.0 $\pm$ 9.81 (11) (127-160)	93.7 $\pm$ 4.37 (6) (88-99)
Females	74.4 $\pm$ 5.20 (11) (69-88)	85.0 $\pm$ 2.94 (4) (81-88)	-- (2) (98+ -113)	73.7 $\pm$ 3.27 (14) (67-79)	69.0 $\pm$ 2.83 (2) (67-71)
Maximum length (mm)					
Total (SVL)					
Males	749 (429)	928 (517)	1,636 (732)	1,338 (675)	890 (590)
Females	424 (309)	992 (705)	674 (436)	649 (475)	664+ (578)
Tail length/total					
Males	0.41 $\pm$ 0.02 (6) (0.37-0.43)	0.41 $\pm$ 0.026 (5) (0.38-0.44)	0.55 $\pm$ 0.007 (2) (0.54-0.55)	0.47 $\pm$ 0.032 (12) (0.41-0.51)	0.33 $\pm$ 0.01 (6) 0.30-0.34
Females	0.26 $\pm$ 0.01 (11) (0.24-0.28)	0.29 $\pm$ 0.005 (3) (0.29-0.30)	0.35 $\pm$ 0.0 (2) (0.35)	0.28 $\pm$ 0.015 (13) (0.24-0.30)	0.26 $\pm$ 0.01 (2) 0.25-0.26
Maxillary teeth	22 + 2-28 + 2 23.9 $\pm$ 2 (16)	19 + 2-21 + 2 19.9 + 2 (8)	20 + 2-23 + 2 21.5 + 2 (4)	17 + 2-28 + 2 23.7 + 2 (28)	20 + 2-24 + 2 21.7 + 2 (9)
Eye diameter/Eye-nostril distance	1.19 $\pm$ 0.12 1.05-1.45 (13)	1.12 $\pm$ 0.10 0.96-1.25 (6)	1.25 $\pm$ 0.11 1.16-1.38 (3)	1.10 $\pm$ 0.16 0.94-1.44 (16)	0.88 $\pm$ 0.06 0.77-0.94 (5)

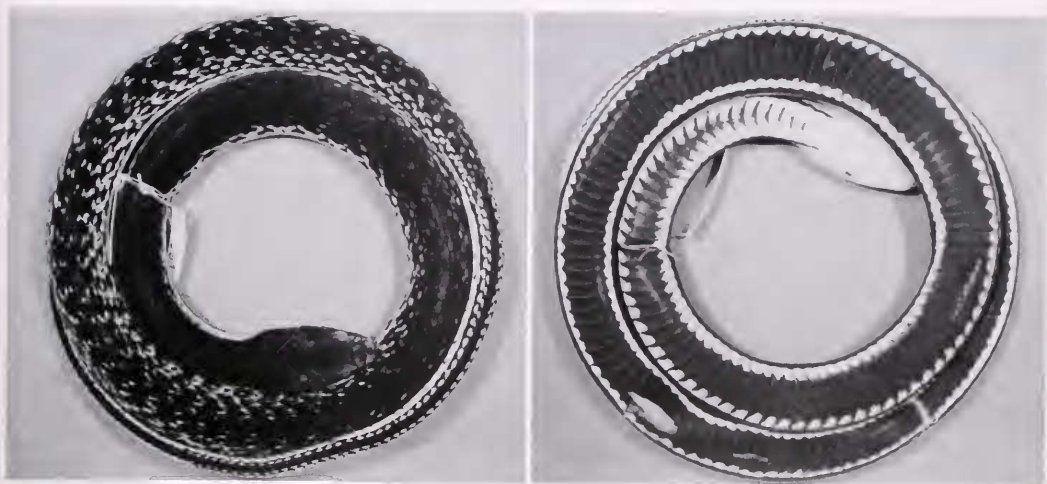


Figure 14. *Liopholidophis doliocercus* (Peracca) from the RNP. Left: MCZ 180403 (female) in dorsal view. Right: Same specimen in ventral view showing the distinctive ventral pattern. The general dorsal suffusion with black pigment seen in this specimen was observed in several females.

mized (Guibé, 1958), in lacking a black stripe on dorsal rows 2–3 (present in *sexlineatus*, subject to some variation; see species account) and in the distinctive uniformly black venter with white ventrolateral stripes (never uniformly black or with white ventrolateral stripes in *sexlineatus*). Species of the *stumpffi* group have 19 scale rows at midbody.

*Liopholidophis doliocercus* is most easily confused with *L. grandidieri* but differs from *grandidieri* in having fewer subcaudal scales (140–164 vs. 215–221, respectively, in males; 81–88 vs. more than 100 [98+–113], respectively, in females) and correspondingly shorter tail (Table 1). The two species also differ in ventral and dorsal patterns. In *Liopholidophis doliocercus* (Figs. 13–14), the central  $\frac{2}{3}$  of each ventral scale is solid black, bordered on either side by a large squarish white dot near the lateral edges of the ventral scales. The white dots of successive scales align to form a regular white stripe on either side of the venter from the anterior portion of the body to the tail tip, thus giving *dolicercus* a highly distinctive, unusual ventral pattern (Fig. 14). Lateral to the ventral white stripes, a bold black line with regular

edges occupies the extreme lateral edges of the ventral scales and the lower half of dorsal row 1; these stripes begin just behind the jaw angle, are briefly interrupted at the vent, and continue to the tail tip at the junction of the subcaudals and first dorsal caudal scale row. Thus, the venter in *L. doliocercus* appears black but bordered on either side by paired white and black stripes (Fig. 14). *Liopholidophis doliocercus* lacks a lateral black stripe on dorsal rows 2 + 3. In *L. grandidieri* (Figs. 18, 20), the entire venter is black except where broken anteriorly and posteriorly by light pigment (no white stripe at lateral edges of ventrals); there is no discrete black stripe on lateral edges of ventrals and lower  $\frac{1}{2}$  of dorsal row 1; and *grandidieri* has a black stripe on rows 2 + 3 (discrete on at least the posterior  $\frac{1}{3}$  of the body [usually more] and anteriorly as well).

*Distribution.* Definitely known from the type locality, Andrangoloaka (see "Remarks"), from the RNP, and from Moramanga (Boettger, 1898:25, 1913:312; Appendix). All are middle-elevation localities on the central part of the eastern escarpment (Fig. 3). Within the RNP, *Liopholidophis doliocercus* has been found at

Talatakely and Miaranony and from approximately 800–1,050 m elevation.

*Description.* The following description is based on examination of eight specimens and color slides of the holotype. Measurements, proportions, and scutellation are summarized in Table 1. Dorsal scales smooth, lacking apical pits, in 17–17–15 rows. Scale reduction by fusion of rows 3 + 4 at the level of ventrals 90–101 (N = 7, including both sexes). Anal plate divided. Tail length strongly sexually dimorphic: 38–44% of total length in males, 29–30% in females. Largest specimen a female (MCZ 180408), 992 mm total length, 287 mm tail length; largest male (MCZ 180405) 928 mm total length, 411 mm tail length. Ventrals 156–160 in males, 143–150 in females. Subcaudals 140–164 in males, 81–88 in females. Supralabials 8 with 4–5 touching eye (N = 7; one specimen has 9 with 5–6 touching eye on one side only). Infralabials 9–9 (N = 2), 10–10 (4), or 10–11 (1), the first pair in contact behind the mental, 1–4 or 1–5 touching an anterior genial, 4–5 or 5–6 touching a posterior genial. Anterior genials approximately equal to, or slightly longer or shorter than, posterior genials. Minute scale pits or tubercles visible under high magnification on many head plates.

Rostral visible from above, about 1.5 times wider than high. Paired internasals, each slightly wider than long, 60–70% as long as prefrontals. Paired prefrontals, each wider than long, in contact with each other and with frontal, supraocular, preocular, loreal, postnasal, and internasal. Frontal pentagonal. Loreals squarish, approximately as high as wide, separated from eye by single preocular, which is much taller than wide, and expanded dorsally and ventrally. Two postoculars (three in the holotype *vide* Peracca, 1892). Temporals 1 + 2 + 3.

Body rounded, somewhat stocky in females, tending toward slightly higher than wide and more gracile in males; ventrolateral edge of body slightly angulate (males) to more rounded (females). Head distinctly wider than neck in females, only

slightly so in males. Pupil round. Eye approximately equal to or slightly greater than distance between eye and posterior edge of nostril ( $\bar{x} = 1.12 \pm 0.1$ ; range 0.96–1.38; N = 6); approximately 50–60% of snout length.

*Dentition.* Maxillary teeth 19–21 + 2 (N = 8). Diastema essentially absent; gap  $\leq 1$  tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row, twice as large as the posteriormost maxillary teeth; having a rounded anterior surface (except for distal 20–25%, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed. The skull from a prepared skeleton (MCZ 180409, female) has 14–13 (l-r) palatine teeth, 26–27 pterygoid teeth, and 26–27 dentary teeth.

*Hemipenis* (see Fig. 31). Deeply bilobed, noncapitate, acalyculate (entirely spinose), with a basal stalk nearly half the length of the organ. Sulcus spermaticus deeply bifurcate, centrolinal. The organ is considerably larger, proportionately, than the hemipenis of other members of the *sexlineatus* group.

*Coloration in Life.* The uniform black venter bordered on either side by a white stripe, and a black stripe on the suture line between the ventrals and dorsal row 1, are highly distinctive (see "Diagnosis"). In contrast, *Liopholidophis doliocercus* is somewhat variable in dorsal coloration, even within the RNP series. Anteriorly, the dorsum tends to be a more or less uniform brown to yellowish brown (Fig. 15) but usually has indistinct darker markings or reticulations (Fig. 16), or general suffusion of black (Fig. 14). Posteriorly, the dorsal coloration tends to be disrupted into a light brown or yellowish brown ground color, with complex black or dark brown blotches or mottling. In some specimens, the posterior mottling takes the form of vague chevrons; in others, it tends to form offset middorsal irregular spots, with irregular markings laterally (Figs. 15, 17). In two females (MCZ 180403 and 180408), the

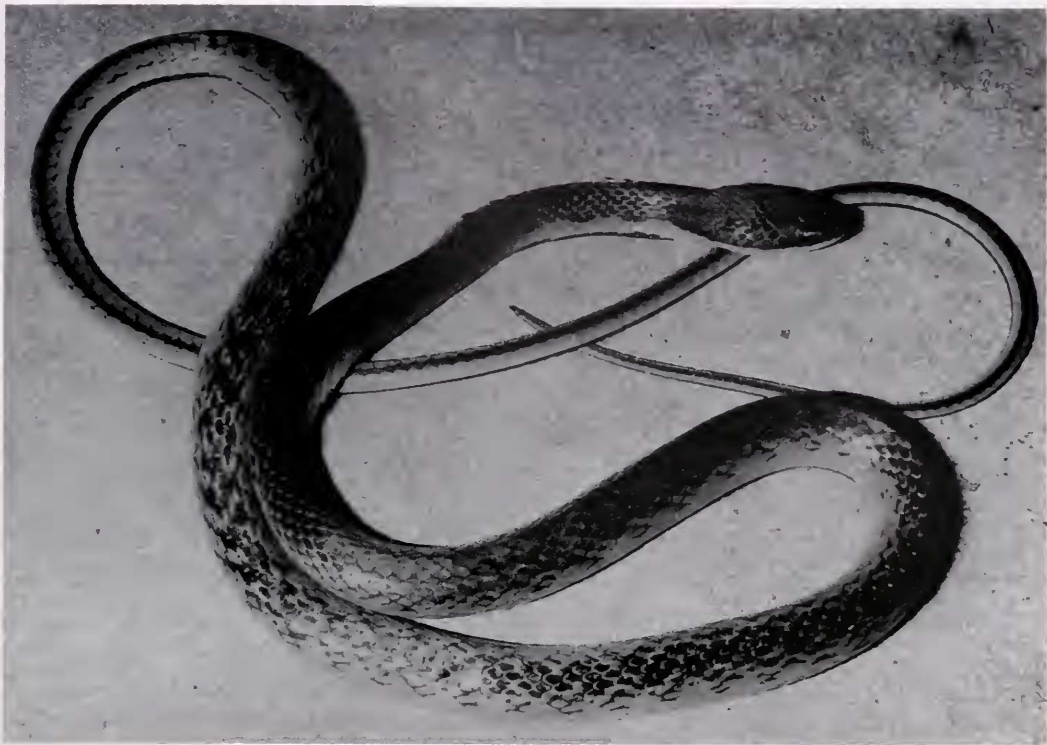


Figure 15. *Liopholidophis doliocercus* (Peracca), a male (MCZ 180407) from the RNP. The chevron-shaped blotches on the posterior dorsum are characteristic of many males (see text).

dorsum has a general suffusion of black pigment (Fig. 14), obscuring the pattern except for occasional light areas on individual scales. The general dorsal color tones are lighter, and pattern more evident, in four males than in four females.

Color notes from life for MCZ 180403 (female) are as follows: Middorsum black. Flanks mottled with black and tan/yellowish brown (yellowish on rows 1–3 anteriorly, 1–5 posteriorly). Top of head posterior to eyes black; anterior to eyes mottled with black and yellowish brown. Upper labials yellowish cream. Lower labials and throat creamy white. Pupil round, iris brown. Ventral pattern: large central area of each ventral scale black, with lateral creamy white border; black stripe on extreme outer edge of each ventral and ventral  $\frac{1}{2}$  of scale row 1. Overall, the venter

appears black with a creamy white stripe and a black stripe down either side. Ventral surface of tail patterned similarly. Lateral portion of tail tan to yellowish brown.

*Coloration in Preservative.* Top of head down to upper edge of supralabials brown, usually suffused or irregularly spotted with black. Upper edge of supralabials and adjacent dorsal head scales with dense black pigment, forming distinct narrow stripe posterior to eye covering lower postocular, lower portion of temporal scales, and up to  $\frac{1}{2}$  of last 2 supralabials; stripe continuing onto anterior body on scale row 4 (dropping to 3 shortly behind head) and becoming discontinuous at level of ventrals 5–10. Other than dorsally bordering black pigment and light brown suffusion anteriorly and/or dorsally, supralabials are immaculate creamy white. Infralabials, mental,

gulars, and preventrals immaculate cream-colored.

Anterior dorsum except for lower 3 dorsal rows usually with suffusion of black, especially in females, in which black may be the dominant pigment (one female, MCZ 180403, is entirely black anteriorly). Postocular black stripe continues on anterior body as a black line on row 4 immediately behind head, dropping to row 3, continuing as a series of irregular dashes along suture between rows 3 and 4 for virtually entire length of body (posteriorly often not discretely separate from general dorsal mottling). Posteriorly, dorsal brown coloration breaks up, at first by lightening of pigment on more lateral dorsal scale rows, then on medial rows. The general effect for most individuals is a more or less unicolor anterior dorsum and a more mottled posterior. With breakup of dorsal color, black pigment retained along lateral scale sutures, forming irregular reticulations.

Venter black, bordered at lateral edges of ventrals by discrete cream stripe and, along suture between ventral scutes and first dorsal row, a regular narrow black stripe (covering about  $\frac{1}{2}$ , or slightly more, of first dorsal row) (Fig. 14). In the RNP sample, the edges of the ventrolateral cream stripe are very regular; in the only non-RNP specimen examined (SMF 17575), the medial edges of the stripe are jagged, as they appear to be in the holotype from the same region (Fig. 13). Ventral surface of tail with median black stripe bordered laterally by cream stripes (Fig. 14).

*Natural History.* *Liopholidophis doliocercus* is diurnal and terrestrial. The species was infrequently encountered in the RNP (seven specimens). All were found in relatively undisturbed forest on the trail system at Talatakely, except for one collected in primary montane rainforest at Miaranony. Specimens were obtained November to January between 0900 and 1530 hr.

A large female collected 2 January 1993 at 1300 hr on the ground by a trail made

no attempt to bite, nor even to resist capture. Several specimens collected by me personally were very slow, almost lethargic, snakes upon capture. Two specimens collected by others were reported to bite, and one was said to be fast-moving.

One specimen of *Liopholidophis doliocercus* contained food: MCZ 180407 (SVL 514 mm) contained one *Plethodontohyla alluaudi*, a small terrestrial (leaf-litter) microhylid frog, swallowed tail first.

Three females in the RNP sample were gravid. MCZ 180403 (SVL 543 mm), collected 15 November, contained five large, yolked, nonoviductal eggs. MCZ 180404 (SVL 634 mm) and MCZ 180408 (SVL 705 mm), collected 10 December and 2 January, contained five and seven shelled eggs, respectively; no embryo was detected in an egg removed from each of these specimens. Based solely on the presence of shelled oviductal eggs, *Liopholidophis doliocercus* is assumed to be oviparous (but see Blackburn, 1993, for cautionary notes).

*Remarks.* Peracca's (1892) description of *Liopholidophis doliocercus* is incomparably good for the period, its only limitation being that it was based only on the male holotype. The collector of the type is not registered in the collection ledgers of the Torino museum (Elter, 1981; verified from photocopies of the catalog pages, which list Peracca as the donor). Peracca stated that the collection from which the type of *dolicercus* came "was donated to the zoological museum of Torino" (Peracca, 1892:5) and, later, for the same collection "a rich collection of reptiles and amphibians from Madagascar arriving at the beginning of the current year . . . comes from the environs of Andrangoloka [=Andrangoloaka] and from the nearby Umbi valley" (Peracca, 1893:5). Several Madagascan reptiles in the Torino collection were donated by a [Giuseppe] Pittarelli (Elter, 1981). Pittarelli lived in Moraman-ga, a town in the vicinity of Andrangoloka, around the turn of the century, and also collected invertebrates for the Torino museum (Nobili, 1905). Peracca possibly





Figure 16. *Liopholidophis dolicoercus* (Peracca), a female (MCZ 180408) from the RNP. In females, the dorsum is often suffused with black pigment or forms a network, as in this specimen, and discrete blotches are usually difficult to discern (cf. Figures 14–15).

obtained Madagascan specimens, including the type of *dolicoercus*, from him.

According to Charles P. Blanc (in litt.; see also Glaw and Vences, 1994:471), who visited the type locality many years ago, Andrangoloaka was on the eastern side of Lake Mantasoa at 1,386 m elevation (47°55'E, 19°02'S, and therefore not "near Manjakandriana," a town well to the northwest of Lake Mantasoa, as reported by Blommers-Schlösser and Blanc, 1991: e.g., p. 233).<sup>6</sup> Originally dense rainforest,

the site has been logged and is now submerged as a result of dam construction. "Umbi" is probably a transliteration of the Malagasy word *Ombi* ("cow"). Neither

ordinates for this locality and others might be engendered by comparison of recent sources with older French sources. For example, Grandidier (1893:295) gave slightly different coordinates for Andrangoloaka than given by the Defense Mapping Agency (1989). The confusion is resolved by realization that French works around the turn of the century commonly used a coordinate system based on the Paris meridian, rather than the Greenwich meridian, as in common use today.

The variant spellings "Andrangoloka," "Andrangolaoka," and "Andrangoloaka" for this locality are commonly seen. "Andrangoloaka" seems to be more consistently used in "period" works (e.g., Grandidier, 1893; Ahl, 1928) and is commonly found in compendia today (e.g., Defense Mapping Agency, 1989; Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994).

<sup>6</sup> Carleton and Schmidt (1990:11; as "Andrangolaoka"), apparently following MacPhee (1987:38; as "Moramanga; Andrangoloaka"), gave the elevation as 950 m, the approximate elevation of Moramanga. But Andrangoloaka itself is farther west and at a higher elevation. Grandidier (1893: accompanying map "Nord-est") gave 1,410 m for Andrangoloaka, closer to Blanc's estimate. Some confusion about co-



Figure 17. *Liopholidophis doliocercus* (Peracca) from the RNP. MCZ 180407 (male).

Blanc nor I succeeded in finding the "Ombi River" on maps or in gazetteers.

Few specimens of *dolicocercus* seem to have been obtained since its description. Other than the RNP series, I am aware only of the type (Peracca, 1892) and a specimen obtained by Boettger (1898, 1913; Appendix). Boulenger (1893, 1896) referred two females in the BMNH to *L. doliocercus*, but these are actually the very similar species, *L. grandidieri* (discussed later). *Liopholidophis doliocercus* was recognized as a distinctive valid species by various workers from the time of its description (e.g., Mocquard, 1904, 1909; Boulenger, 1893, 1896, 1915; Boettger, 1898, 1913; Parker, 1925; Werner, 1929) but appears not to have been mentioned in the literature between Werner's (1929) listing in a checklist and Guibé's (1958) placing it in the synonymy of *L. sexlineatus* (see also Brygoo, 1983). However, *Liopholidophis doliocercus* bears little resemblance to *L. sexlineatus* in coloration or pattern, which is apparent from a reading of Peracca's (1892) description, and it differs from *sexlineatus* in body proportions, habitus, hemipenial morphology (see below), and macrohabitat association. Scale

counts in the two species are similar (Table 1), which probably led Guibé to synonymize them. Because of substantive differences of coloration, pattern, hemipenial morphology, and body proportions, I resurrect *Liopholidophis doliocercus* from the synonymy of *Liopholidophis sexlineatus*. As Peracca's description of the type of *dolicocercus* is unusually complete, I did not examine the holotype directly but did study a series of color transparencies of it (including the head, dorsum, and venter; cf. Fig. 13). The RNP series unquestionably conforms to Peracca's (1892) *dolicocercus*.

An apparent author's or printer's correction to the description of *Liopholidophis doliocercus* requires comment. A reprint of Peracca's article in the MCZ herpetology department library, and the bound journal copy in the Museum of Comparative Zoology (Ernst Mayr) Library, have the subcaudal count in the description (Peracca, 1892:2) scratched through in ink and "corrected" by hand to 164 (original printed figure apparently "329"). The handwriting of the correction in both sources is identical and in a rather archaic script. I subsequently checked another copy of the journal in the library at the Marine Biological Laboratory, Woods Hole; the same correction in the identical handwriting was found. I infer that these sources were corrected either by Peracca himself or at his or the printer's direction. Similar corrections were made in all three sources for the description of *Tachymenis boulengerii* in the same paper.

The ventral black coloration of *Liopholidophis doliocercus* possibly develops ontogenetically, although no small subadults from the RNP are available to be certain. Ontogenetic development is suggested by the ventral pattern in the male holotype, which, at 427 mm total length (265 mm SVL; Peracca, 1892), is about  $\frac{1}{2}$  the length of any other male *dolicocercus* examined (observations from magnification of color transparencies of the type). In the type, only the posterior  $\frac{1}{2}$  of the venter is solid black; anteriorly, the black

pigment is broken up (increasingly, posterior to anterior) so that the anterior ventral scutes have, at most, a central region heavily stippled with black, yielding a grayish overall appearance. If this interpretation is correct, small juveniles of *dolicocercus* possibly have immaculate, or only posteriorly darkened, venters. Given the similarity in the ventral patterns of *dolicocercus* and *grandidieri*, the last species possibly also undergoes a similar ontogenetic transformation.

*Liopholidophis dolicocercus* is the only species of the *sexlineatus* group for which males do not appear to attain greater total lengths or SVLs than females (Table 1), but this probably reflects the small sample size of males for this species.

### *Liopholidophis grandidieri*

Mocquard

Figures 12, 18–20

*Tropidonotus* [*Dromicus*] *dolicocercus* [sic] (not of Peracca, 1892): Boulenger, 1893:246–247, 1896:607, specimens a and b (misidentification; further discussed later).

*Liopholidophis grandidieri* Mocquard, 1904:304. (Type locality, "l'embouchure du Saint-Augustin" [mouth of the Saint-Augustin River], in error). Holotype, MNHN 02-103 [examined] (Figs. 18–19). Boettger, 1913:372; Parker, 1925:392; Werner, 1929:11; Guibé, 1958:217–218; Brygoo, 1983:55, 1987:24; UICN/PNUE/WWF, 1990:223; Glaw and Vences, 1992:266, 1994:338; Nicoll and Langrand, 1989:130.

*Tropidonotus grandidieri* (Mocquard): Boulenger, 1915:373.

**Holotype.** MNHN 02-103 (Figs. 18–19), an adult male in fair condition; 1,636 mm total length, 904 mm tail length (55% of total length), 171 ventrals, 221 subcaudals, divided anal plate, 22 + 2 maxillary teeth.

**Diagnosis.** A species of *Liopholidophis* characterized by more than 200 subcaudals in males, more than 100 subcaudals in females; tail >50% of total length in males (35% in females); venter (except for anterior ventral plates) entirely black, including the anal plate, and not bordered by a marginal white stripe; lateral black stripe on dorsal rows 2–4 anteriorly and

2–3 posteriorly, but dark dorsal stripes otherwise lacking. These features distinguish *Liopholidophis grandidieri* from all species of *Liopholidophis*, none of which have such proportionally long tails; all species but *dolicocercus* have dorsal stripes (light or dark) on scale rows other than 2 + 3. *Liopholidophis grandidieri* is most easily confused with *L. dolicocercus*; distinguishing features are given in the account for that species.

**Distribution** (Fig. 3). Known definitely from the RNP (Mt. Maharira) and from Ambohitombo Forest, a locality well known from specimens collected by Forsyth Major (e.g., Boulenger, 1896; Major, 1896). The type locality, "l'embouchure du Saint-Augustin" (mouth of the Saint-Augustin River), is in the arid southwestern sector of the country (23°33'S, 43°46'E; Fig. 3) and almost certainly in error. All other specimens are from the eastern rain-forest belt (Appendix). The type of *grandidieri* was the only specimen recognized until recently. The two documented localities are approximately 70 km apart in the central part of the eastern escarpment (Fig. 3).

The descriptor "eastern Imerina" (locality for BMNH 95.10.29.52) refers to the territory on the eastern edge of the escarpment between approximately parallels 18° and 21°, the Imerina being one of the indigenous peoples of the central plateau (see, e.g., Gallieni, 1908:pl. 6). I have tried, without success, to verify the documentation and localities for the records listed by the UICN/PNUE/WWF (1990:223) as "three new specimens from the eastern forests."

The single specimen from the RNP was collected near the highest point in the park, 1,375 m (Mt. Maharira; see later). BMNH 95.7.4.32 is from Ambohitombo Forest, presumably near the town of that name, which is at approximately 1,200 m elevation.

**Description.** The following description is based on examination of two males (including the holotype) and two females. Measurements, proportions, and scutella-

tion are summarized in Table 1. Largest specimen the male holotype, 1,636 mm total length, 904 mm tail length; largest female (BMNH 95.7.4.32) 674 mm total length, 238 mm tail length. Tail length strongly sexually dimorphic, 54–55% of total length in males, 34–35% in females (Figs. 18, 20). Dorsal scales smooth, lacking apical pits, in 17–17–15 rows. Scale row reduction from 17 to 15 rows by fusion of rows 3 + 4 at the level of ventrals 92–112 (N = 3). Ventrals 169–171 in males, 147–161 in females. Anal plate divided. Subcaudals 215–221 in males, 113 in female with complete tail (98+ in female with incomplete tail). Eight upper labials with 4–5 touching eye; 9 lower labials, the first pair in contact behind the mental, 1–4 touching an anterior genial, 4–5 touching a posterior genial. Anterior genials shorter than posterior genials. Two postoculars; temporals 1 + 2.

Body slightly higher than wide; ventrolateral edge of body angulate. Head slightly wider than neck. Pupil round. Eye relatively large, its diameter greater than distance between eye and posterior edge of nostril ( $\bar{x} = 1.25 \pm 0.1$ ; range 1.16–1.38; N = 3), its diameter 60–65% of the distance from anterior edge of eye to tip of snout. Scattered minute pits and tubercles appear to be present on the anterior head plates.

*Dentition.* Maxillary teeth 20–23 + 2 (N = 4). Diastema short or absent, one tooth width or less. The ungrooved fangs are less than twice as large as the posteriormost maxillary teeth, have a flattened knifelike posterior surface, and have a rounded anterior surface except for the distal tip, which is slightly compressed and has a short cutting edge. The fangs are essentially in line with the prefang teeth (i.e., not offset). A prepared skull (MCZ 180297, male) has 20–23 maxillary teeth, 16–18 palatine teeth, 25–29 pterygoid teeth, and 30 right dentary teeth (left damaged); the diastema in this specimen is about the width of the preceding teeth, and the fangs are not offset.

*Hemipenis* (Fig. 32). Deeply bilobed, noncapitate, acalyculate (entirely spinose),

with a basal stalk comprising slightly less than  $\frac{1}{2}$  the length of the organ. Sulcus spermaticus deeply bifurcate, centrolinal.

*Coloration in Life.* I have not seen *Lio-pholidophis grandidieri* in life. However, given the overall exceedingly similar patterns of *grandidieri* and *dolicocercus*, I suspect that the two species have similar coloration in life (see species account for *dolicocercus*).

*Coloration in Preservative* (MCZ 180297). The specimen is perhaps somewhat excessively darkened as a preservation artifact; its pattern is less distinct than that of the holotype. Anteriorly, a mid-dorsal series of irregular blotches or paired spots, separated by whitish interspaces. The dorsum rather abruptly darkens shortly after the neck region, and most of the dorsum appears blackish. Many dorsal scales of all rows except the first have distinctly white borders; these are more evident anteriorly, posteriorly becoming obscured by increasing black pigment. An indistinct brownish streak is present on the flanks, and a brownish gray streak on scale rows 1–2. Black lateral stripe continuous with postocular stripe, on rows 3–5 immediately behind head, soon dropping to rows 2–4 for much of the body, and to adjacent portions of rows 2–3 posteriorly; the lateral stripe is indistinct and disrupted anteriorly, but very distinct, continuous, and with regular borders posteriorly. Throat and several anterior ventrals white, but remainder of venter and lower part of scale row 1 solid black; anal plates black. Top of head brownish; black postocular stripe continuous with lateral black stripe. Some black pigment on upper edges of supralabials, preoculars, loreals, nasals, and rostral; supralabials, infralabials, and gular region otherwise white. Tail with a mid-dorsal, midventral, and a pair of ventrolateral black stripes (at border between subcaudals and dorsal caudal scales); the midventral stripe becomes thinned and broken toward the tip, but stripes otherwise continue to the tip. Subcaudals otherwise white; dorsal caudals otherwise brownish.

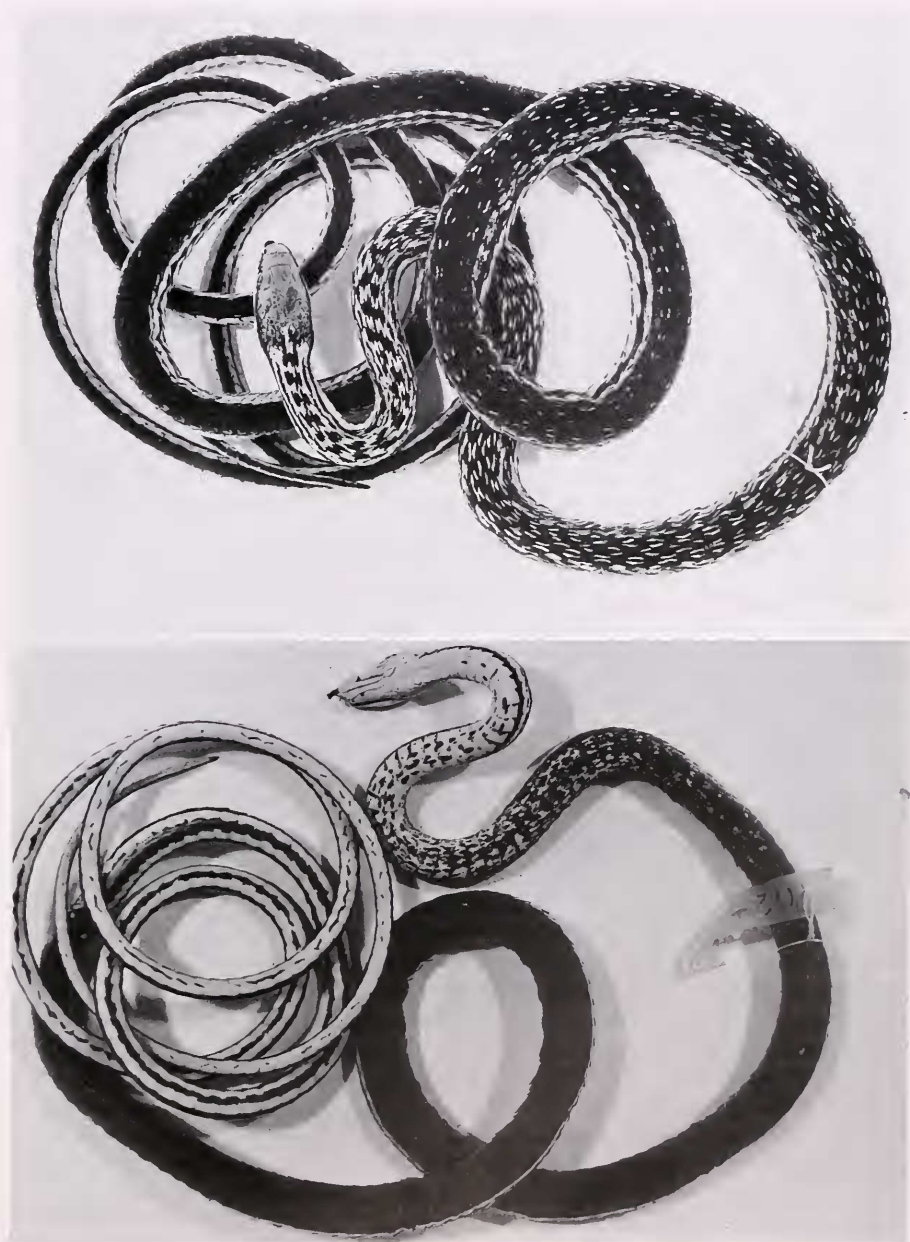


Figure 18. *Liopholidophis grandidieri* Mocquard, dorsal and ventral views of the male holotype (MNHN 02-103).

The two BMNH females (Fig. 20) and the holotype (Figs. 18-19) of *grandidieri* are similar to MCZ 180297, except in having somewhat more distinct lateral stripes and in tending to have the black ventral

coloration broken up somewhat more anteriorly and posteriorly. Many of the dorsal scales of these specimens also have vivid white borders, as in MCZ 180297. The black stripe on the subcaudal scales is

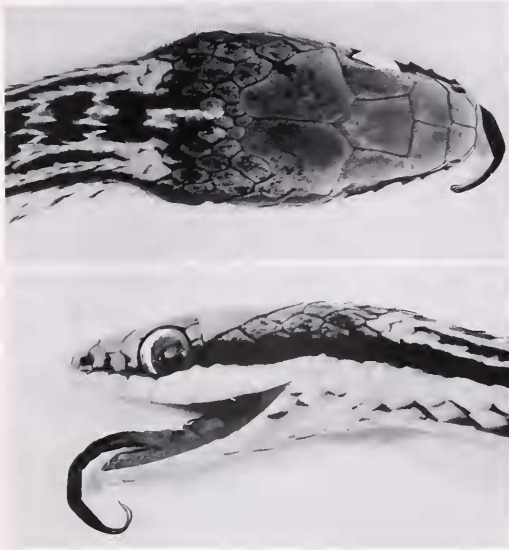


Figure 19. *Liopholidophis grandidieri* Mocquard, dorsal and lateral views of the head of the holotype (MNHN 02-103).

somewhat variable, being more or less continuous to the tail tip (MCZ 180297), essentially absent (BMNH 95.7.4.32, 95.10.29.52; a few blackened suture lines) or continuous anteriorly but absent posteriorly (MNHN 02-103).

*Natural History.* The RNP specimen was collected 13 April 1992 during the day near the summit of Mt. Maharira, a granitic massif with expanses of bare rock, grassy areas, and low scrubby forest (probably resulting from thin soil over bedrock).

Two females, BMNH 95.7.4.32 (SVL 436 mm) and 95.10.29.52 (SVL 412 mm), have large oviductal eggs (five and four, respectively, as ascertained by palpating) covered by a thickened leathery shell. BMNH 95.7.4.32 was obtained at Ambohimombo by Forsyth Major, who collected there 12–24 January 1895 (Carleton and Schmidt, 1990:table 1). One egg from BMNH 95.7.4.32 contained an embryo in Zehr (1962) stage approximately 23–24. The relatively advanced embryo surrounded by a leathery shell suggests oviparity in *grandidieri* according to criteria outlined by Blackburn (1993).

*Remarks.* *Liopholidophis grandidieri* was described along with a heterogeneous assortment of amphibians and reptiles from Africa and South America (Mocquard, 1904), and neither a collector nor donor of the type was stated. The only other Malagasy species described in the same paper, *Pseudoxyrhopus dubius* (= *tritaeniatus*; cf. Raxworthy and Nussbaum, 1994), was said to have been “sent to the [Paris] Museum, without indication of locality, by M. Rousson, explorer” (Mocquard, 1904:306). *Liopholidophis grandidieri* was described during a period of accelerated French expansion and exploration in Madagascar (Gallieni, 1908), and the type may have been obtained by any number of French political administrators, explorers, or medical or military personnel on the island at the time.<sup>7</sup> The type locality, Saint Augustine Bay, was a major port and shipping point during the period (see, e.g., Bastard, 1898), and the type was probably sent to Paris with the “locality” recorded as the shipping point.

Two females of *Liopholidophis grandidieri* were erroneously referred to *L. dolicoercus* by Boulenger (1893:246–247, 1896:607): BMNH 95.10.29.52, collected by the Reverend R. Baron in “East Imerina,” and BMNH 95.7.4.32 (Fig. 20), collected by Dr. Forsyth Major in the “Ambohimombo Forest.” That these are the specimens Boulenger had in hand is suggested by the associated collectors, locality data, measurements (for 95.10.29.52), sex, ventral and subcaudal counts, and ventral pattern (described in detail later), as reported by Boulenger (1893, 1896). My

<sup>7</sup> The Bulletin du Muséum d’Histoire Naturelle during this period contains numerous references to collections received from Madagascar. For example, volume 4 (1898, no. 2, p. 4), includes the following: “. . . the arrival of a crate sent from Tamatave [=Toamasina] by Captain Ardouin and containing some reptiles, diverse arthropods, several molluses, and two Hova skulls” (the Hova being one of the indigenous peoples). Rarely, it seems, were these notices sufficient in themselves to relate to specific collections or specimens.

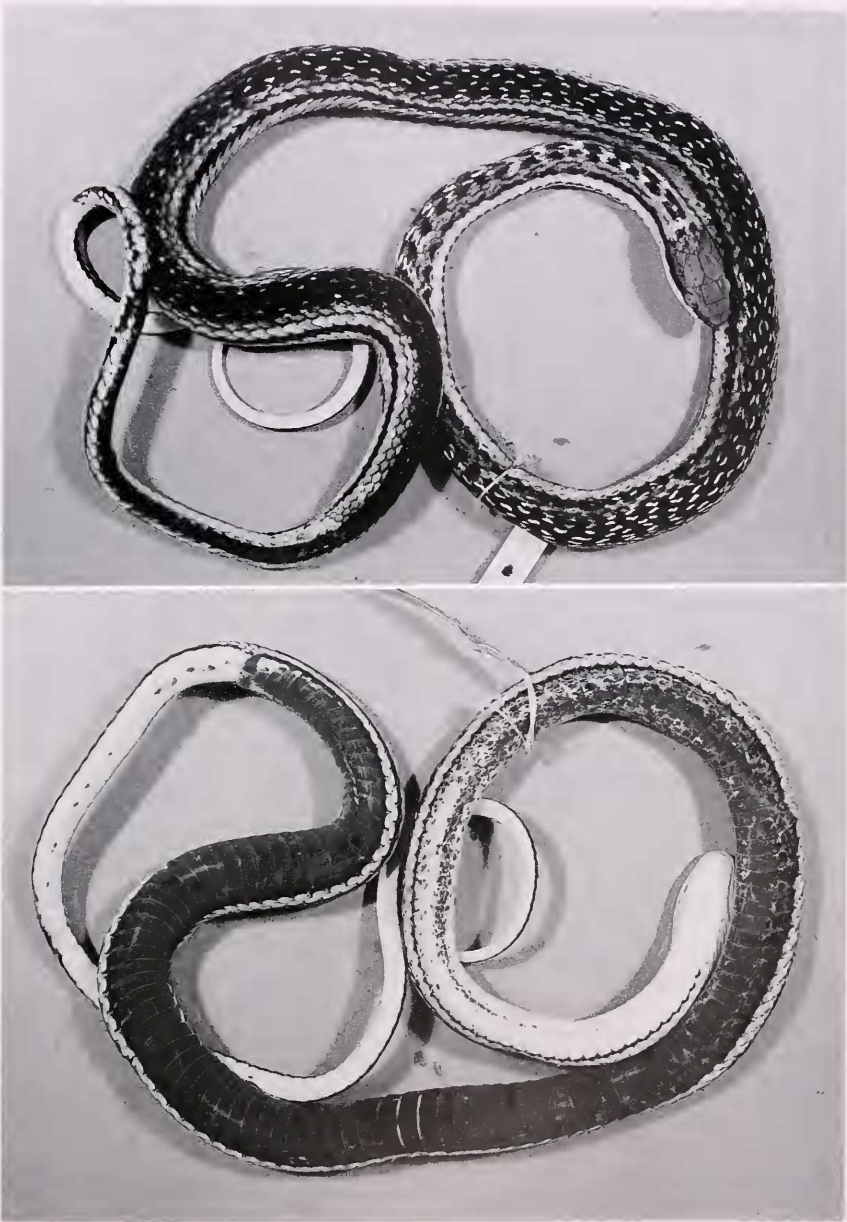


Figure 20. *Liopholidophis grandidieri* Mocquard. Dorsal and ventral views of a female from "Ambohitombo Forest" (BMNH 95.7.4.32). This specimen was referred to (*Liopholidophis*) *dolicocercus* by Boulenger (1896:607; specimen b).

counts for ventrals and subcaudals differ from Boulenger's by at most two (Table 1), and those differences may be accounted for by a somewhat damaged tail in BMNH

95.7.4.32 and the inclusion of preentrals in the ventral counts given by Boulenger.

Boulenger's erroneous referral of these specimens to *dolicocercus* is understand-

able in view of the fact that he was comparing two females with the description of the male holotype of *dolicocercus*, in a genus known to exhibit exaggerated sexual dimorphism in subcaudal counts. Boulenger failed to note Peracca's explicit description of one of the diagnostic pattern differences between *dolicocercus* and *grandidieri*: "... [in *L. dolicocercus*] a black line ... runs in part along the margins of the ventrals, in part on the inferior series of the scales of the body. This line is bordered with yellowish white along its inferior margin" [i.e., at the lateral edges of the ventral scutes; emphasis added] (Peracca, 1892:2). The two BMNH specimens have the alternative pattern characteristic of *grandidieri*, viz., an entirely black venter (no white stripes), separated by a light interspace from lateral black stripes on dorsal rows 2 + 3: "belly black, separated from the lateral streak by a yellowish interspace or streak" (Boulenger, 1893:247). Significantly, Boulenger does not mention the two ventral pattern features diagnostic of *dolicocercus* (see "Diagnosis" in the *dolicocercus* account for other differences).

*Liopholidophis sexlineatus*  
(Günther)

Figures 12, 21

*Dromicus sexlineatus* Günther, 1882:264 (Type locality, "Eastern Betsileo"). Syntypes, The Natural History Museum, London (BMNH) 1946.1.13.17–19 [examined].

*Dromicus macrocercus* Günther, 1882:265 (Type locality, "Eastern Betsileo"). Syntypes, BMNH 1946.1.13.28–30 [28 not seen]. Peracca, 1892:2. Boulenger, 1893:246 (synonym of *Tropidonotus sexlineatus*). Mocquard, 1909:95 (synonym of *Liopholidophis sexlineatus*).

*Leptophis varius* Fischer, 1884:36 (Type locality, "Madagascar"). Syntypes, five specimens in the Natural History Museum in Hamburg, nos. 1174–75 *vide* Fischer (1884:38) [not seen].<sup>8</sup> Boulenger,

1893:246 (synonym of *Tropidonotus sexlineatus*). Guibé, 1958:246 (synonym of *Liopholidophis sexlineatus*).

*Dromicus dolicocercus* Peracca, 1892:1 (Type locality, "Valle dell'Umbi [Andrangoloka]"); Guibé, 1958 (synonym of *Liopholidophis sexlineatus*). Here considered a valid taxon.

*Tropidonotus sexlineatus* (Günther): Boulenger, 1893:246, 1896:607, 1915:373. Jourdran, 1903:34.

*Liopholidophis sexlineatus* (Günther): Mocquard, 1904:303, 305; 1909:43, 95; Boettger, 1913:372; Parker, 1925:392; Werner, 1929:11; Guibé, 1958:216; Domergue, 1969:19; Brygoo, 1983:55, 1987:24; UICN/PNUE/WWF, 1990:223; Glaw and Vences, 1992:266, 1994:338; Nicoll and Langrand, 1989:135.

*Syntypes*. BMNH 1946.1.13.17–19 (old numbers 82.5.8.3, 82.5.8.2, and 82.5.8.4, respectively), all three adult females obtained by Rev. W. D. Cowan. Scale counts, measurements, and other data for the syntypes are, respectively, as follows: ventrals: 146, 145, 144 (preceded by 1, 2, and 1 preventrals); subcaudals: 74, 73, 77; anal divided; total lengths (mm): 605, 620, 589; tail lengths (mm): 175, 172, 175 (29%, 28%, 30%, respectively, of total length); maxillary teeth: 23 + 2 in each case.

*Diagnosis*. *Liopholidophis sexlineatus* is distinguished from members of the *stumpffi* group in having 17–17–15 scale rows (vs. 19–19–17). It differs in details of color pattern from *dolicocercus*, *grandidieri*, and *rhadinaea*: venter largely solid black, or solid black with marginal white stripe, in *grandidieri* or *dolicocercus*, respectively; whitish to heavily, but irregularly, splotched with black (never solid black) in *sexlineatus*; three light nape spots

cf. Table 1). Nonetheless, given the difficulty of separating females of *sexlineatus* from both sexes of *pinguis*, some of the syntypes of *varius* could be the same as the later-described taxon *pinguis*. In particular, Fischer's "specimen c" has 92 subcaudals, an unusually high count for *sexlineatus* females, but a typical one for *pinguis* males (Table 1) (assuming a complete tail and correct counts); other details given for this specimen conform to either *pinguis* or *sexlineatus*. Fischer (1884) also alludes to varying development of the lateral and ventrolateral stripes ("often beginning at the middle of the body"), and paired ventral spots, in his series of *varius*; these characteristics also suggest *pinguis* (see species account).

<sup>8</sup> I am blindly following Boulenger (1893) in relegating *varius* to the synonymy of *sexlineatus*, which seems likely for some or all of the syntypes of *varius*. In that case, all of the types would be females or else males with incomplete tails, given their subcaudal counts and relative tail proportions (Fischer, 1884:38;



and dorsolateral light stripe in *rhadinæa* (absent in *sexlineatus*).

*Liopholidophis sexlineatus* is most similar to *L. pinguis* in overall habitus and color pattern. Males of *pinguis* have short tails (<35% total length; <110 subcaudals) compared to males of *sexlineatus* (>40% total length; >120 subcaudals), and the relative eye size of *pinguis* is smaller than that of *sexlineatus* (Table 1). Most specimens of *pinguis* have less distinct stripes on the anterior body than *sexlineatus*, and the venter in the former is usually light-colored (sometimes with edges of ventrals blackened or with a median series of small paired spots); in *sexlineatus*, the stripes are distinct the entire length of the body (flanks may be entirely darkened) and, although the venter may be immaculate, it is often heavily and irregularly splotched with black.

*Distribution* (Fig. 3). Scattered localities on the eastern escarpment and lowlands from the southeastern tip of Madagascar (Glaw and Vences, 1994:336 [map]), north to at least Toamasina (Toamasina Province); a few localities on the high plateau as documented in the Appendix ("Manjakatempo") and as shown by Glaw and Vences (1994:336 [map]). Although seemingly locally abundant where it occurs (personal observations), *Liopholidophis sexlineatus* is recorded from relatively few localities in the literature.

In the RNP region, *Liopholidophis sexlineatus* appears ubiquitous in rice paddies and marshy areas and is known from approximately 500 to 1,130 m elevation.

*Description*. The following description is based on examination of 18 females and 15 males, including types of *Dromicus sexlineatus* and *D. macrocerus*. Measurements, proportions, and scutellation are summarized in Table 1. Largest specimen a male (MCZ 11604), 1,338 mm total length, 663 mm tail length (50% of total); largest female (MCZ 11701) 726 mm total length, 238 mm tail length (33% of total). Tail length strongly sexually dimorphic, 41–51% of total length in males, 24–33% in females. Dorsal scales smooth, lacking

apical pits, in 17–17–15 rows. Scale row reduction from 17 to 15 rows by fusion of rows 3 + 4 at the level of ventrals 90–115 (N = 17; 1 specimen showed fusion of 4 + 5 at the level of 92–95). Ventrals 147–163 in males, 139–148 in females. Anal plate divided. Subcaudals 127–160 in males,<sup>9</sup> 67–91 in females. Eight upper labials with 4–5 touching eye. Lower labials 9–9 (N = 12), 9–10 (8), 10–10 (11), or 11–12 (1), the first pair in contact behind the mental, 1–4 or 1–5 touching an anterior genial, 4–5 or 5–6 touching a posterior genial. Anterior genials shorter than posterior genials. Loreal present. Preocular usually single (occasionally 2). Temporals 1 + 2 (rarely 3 secondary temporals).

Body slightly higher than wide; ventrolateral edge of body rounded in females, slightly more angulate in males. Head wider than neck. Pupil round. Eye relatively small, its diameter approximately equal to or somewhat greater than distance between eye and posterior edge of nostril ( $\bar{x}$  = 1.1 ± 0.16; range 0.95–1.44; N = 16). A few scattered pits on anterior head plates.

*Dentition*. Maxillary teeth 17–26 + 2 (N = 25;  $\bar{x}$  = 23.9 ± 1.9 prefang teeth). Diastema essentially absent; gap <1 tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row, twice as large as the posterior-most maxillary teeth; having a rounded anterior surface (except for distal portion, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed. The skull from a prepared skeleton (MCZ 180332, female) has 15–15 palatine teeth, 34–35 pterygoid teeth, and 34–34 dentary teeth.

*Hemipenis* (Fig. 33). Deeply bilobed (nearly half the length of the organ), non-

<sup>9</sup> One male, MCZ 11605, has unusually low subcaudal (127) and maxillary tooth (17) counts (next highest values 140 and 20, respectively). This possibly represents normal variation within *sexlineatus* but needs clarification with a thorough study of geographic variation in this taxon. MCZ 11605 also has an unusual coloration (see "Remarks") but, unfortunately, lacks precise locality data.

capitate, acalyculate (entirely spinose), with a deeply bifurcate centrolinal sulcus spermaticus that stops short of the tips of the lobes. Distal sulcate tips of the lobes with 8–10 papillae, each surmounted by a spine.

*Coloration in Life (RNP Region), Based on MCZ 180326-35 (see Glaw and Vences, 1994:pl. 348).* Middorsal area five scales wide dark olive brown or medium brown, three rows either side of this olive brown; rows 1–3 grayish brown, but with variable amount of black (generally much black on 2–3, especially anteriorly, with black increasing on 1–3 posteriorly). Edges of scale row 3 and 7–9 often with striking white border (very thin); this more prominent on anterior body, and on dorsal edge of row 3. Extreme outer edge of ventrals black, forming black stripe in conjunction with black pigment on dorsal row 1. Remainder of venter with ground color of dull cream, but often heavily invested with black, especially toward posterior end of body. Top of head dark olive brown. Postorbital bar black. Upper and lower labials, and throat dull whitish.

The pattern of *Liopholidophis sexlineatus* in the RNP area is similar to the color plate in Glaw and Vences (1994:pl. 348), but the colors are more subdued: median dorsal area darker brown, and dorsolateral ground color dull olive brown rather than yellowish brown.

*Coloration in Preservative.* Although the specific epithet refers to six stripes, most specimens I examined have only four distinct stripes, and general darkening of the flanks may obscure the lateral and ventrolateral stripes entirely so that the snake appears to be a brown snake with black flanks. Günther (1882:265) indicated similar variation, stating that *sexlineatus* has "six black longitudinal bands, of which, . . . two or more may be indistinct or disappear altogether." The entire range of variation is seen within the sample from the RNP, and I detected no geographic trend.

When the complete complement of six stripes is present, they are disposed as fol-

lows: (1) a black border on the suture between the ventral plates and dorsal row 1; (2) a facial stripe beginning on the upper edge of the supralabial row, widening as a postocular stripe, continuing onto body, where it usually occupies the lower  $\frac{2}{3}$  of row 3 + upper  $\frac{1}{3}$  of row 2; occasionally involving lower portion of row 4; (3) a stripe, usually indistinct and often absent, on the suture between dorsal rows 6 and 7. In some specimens the entire lower 3 dorsal rows are blackened, or blackened with only a central spot of light pigment in each scale, with the black extending a variable distance onto the ventral plates (Fig. 21). The median 5 dorsal rows are darker brown than more lateral rows (1–6), which are grayish brown. The venter is whitish, but with a highly variable investment of black: most specimens from the RNP have at least the lateral edges of the ventrals black, but often black is the predominant ventral coloration. Additional comments are given in the "Remarks."

*Natural History.* *Liopholidophis sexlineatus* is diurnal and semiaquatic. The species is abundant in rice fields, especially those somewhat overgrown around the edges of paddies, and with a covering of *Azolla* or duckweed. It seems most characteristic of sluggish or standing water, but the species was abundant in tall (0.5 m) grass along one whitewater river with rocky substrate next to rice fields, and two snakes in the same area were in water at the edge of the river. I never observed *L. sexlineatus* in primary or secondary forests, including aquatic habitats therein (small forest streams and pools, larger rivers). *Liopholidophis sexlineatus* was observed in apparently natural habitats only near Sahavondrona, within the RNP. Here, the species was associated with meadows, bogs, and marshes, which, during the rainy season, fill with standing water to depths of up to 0.5 m. The meadows occupied depressions of varying sizes surrounded by higher ground supporting forest and are possibly maintained as meadows by seasonal flooding during part of the year. The meadows near Sahavondrona were filled

with a grass/sedge association and were breeding and/or retreat sites for species of *Heterixalus* spp. (Hyperoliidae), *Ptychadena mascareniensis* (Ranidae), and *Boophis* spp. and *Aglyptodactylus madagascariensis* (Rhacophoridae). *Liopholidophis sexlineatus* is inoffensive and does not bite in defense.

Glaw and Vences (1994:338), citing personal communication from C. Domergue, reported *L. sexlineatus* as ovoviviparous (=viviparous *vide* terminology of Blackburn, 1994), but the basis for the inference was not stated. Given the long egg retention times of many oviparous squamates (Shine, 1983), and the rather stringent criteria that must be met to be assured of correct inference of reproductive mode (Blackburn, 1993), the report of viviparity in *sexlineatus* needs confirmation. I can offer only partial corroboration. Five females in the RNP sample collected 8 December were gravid, with 4–10 embryos (determined by palpation and inspection), as follows: MCZ 180325 (SVL 400 mm; 7 embryos), MCZ 180329 (SVL 452 mm; 10), MCZ 180330 (SVL 333 mm; 4); MCZ 180331 (SVL 408 mm; 7), and MCZ 180334 (SVL 475 mm; 8). In all cases, the developing embryos were surrounded by fetal membranes, but without thickened shell membranes or leathery shell. Two embryos removed from MCZ 180334 were in Zehr (1962) stage 25–26; one removed from MCZ 180329 was approximately stage 24. Because all gravid females were collected at the same time, and none showed any apparently more advanced embryos upon casual inspection, no other embryos were examined directly. Embryos of other species of *Liopholidophis* of comparable stages of development (see species accounts) are invariably surrounded by leathery shells; absence of such a shell in *L. sexlineatus* is taken to confirm the presence of viviparity in this species (but see cautionary notes in Blackburn, 1993).

All dietary items for *Liopholidophis sexlineatus* were frogs. I was drawn to a specimen in a marsh by the loud release calls of a *Ptychadena mascareniensis*,

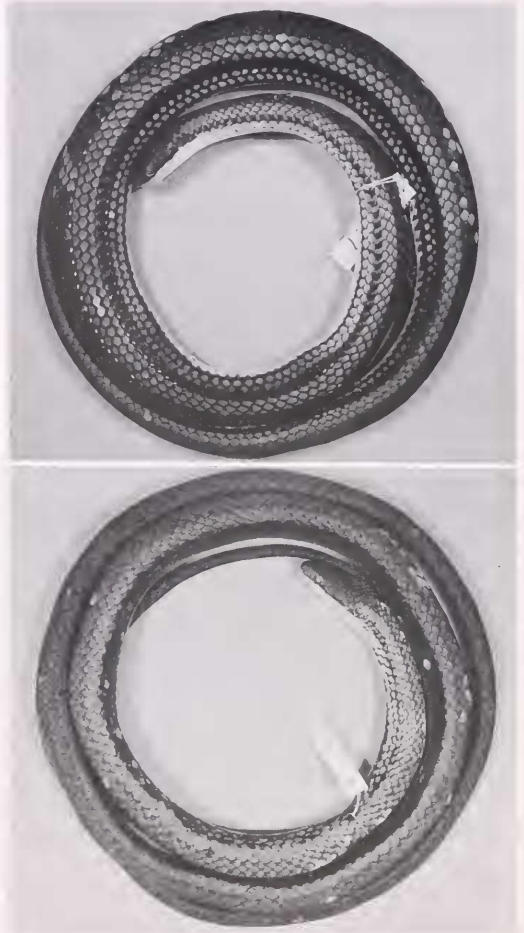


Figure 21. *Liopholidophis sexlineatus* (Günther). Top: Specimen from the RNP (MCZ 180331). Bottom: Specimen from near Midongy du Sud (MCZ 180379). Note the darkening along the suture lines of dorsal rows 1–2 in the former and the complete darkening of the flanks in the specimen from Midongy du Sud, rendering the lateral stripe indiscernible except on the anterior part of the body.

which the snake was eating at 1350 hr on 22 November 1990. The snake was in a relatively open boggy area under a small clump of vegetation; much of the marsh had tall (80–100 cm), dense grass. MCZ 180376 (SVL 439 mm) contained 14–16 *Heterixalus* cf. *madagascariensis*. MCZ 180338 (SVL 472 mm) contained unidentifiable remains of a small frog. Four specimens from Ambatolahy near the RNP col-

lected 8 December 1990 and held in a common collecting bag regurgitated frogs (*Ptychadena mascareniensis*, *Heterixalus betsileo*, and *H. alboguttatus*).

The frogs recorded in the diet of *Liopholidophis sexlineatus*, *Heterixalus* and *Ptychadena*, are the most commonly encountered frogs in the marshes and rice fields that are the major habitats of *sexlineatus*.

*Remarks.* Günther (1882) described females and males of *Liopholidophis sexlineatus* (as *Dromicus sexlineatus* and *D. macrocercus*, respectively) in the same paper, failing to realize that the extraordinary differences in tail length and subcaudal counts manifested sexual dimorphism (of a nature hitherto unknown in snakes). Curiously, he thought he had males and females within the series of syntypes he described as *sexlineatus* (p. 265, comment referring to dimorphism in ventral color). The error was caught by Boulenger (1893: 246), who correctly identified types of *sexlineatus* as females and those of *macrocercus* as males. Boulenger (1893) synonymized the two species and, as first revisor, fixed the name of the taxon as *sexlineatus* (International Commission on Zoological Nomenclature, 1985:article 24[a]).

The type locality, "eastern Betsileo" refers to territory on the eastern edge of the plateau and the adjacent escarpment between approximately parallels 21° and 22°30'S (the Betsileo being one of the indigenous peoples inhabiting this region; see, e.g., Gallieni, 1908:pl. 6). Thus, the syntypes of *sexlineatus* come from the general region of the RNP, but probably from the adjacent plateau rather than from the escarpment itself.

Aside from the variable distinction of the dorsal stripes (see Coloration), the amount and distribution of black pigment in *Liopholidophis sexlineatus* varies considerably. Unfortunately, samples have been insufficient to fully characterize the variation (possibly geographic). Future studies should comprehensively survey the taxon throughout its range to discern whether or not more than one taxon is

involved. The following comments highlight patterns I discerned.

Specimens from Toamasina Province (MCZ 11602–06) have little black pigment on the venter or on dorsal rows 1–2, except for the upper portion of row 2 involved in the lateral stripe and some darkening or spotting along the suture lines between ventral plates. In MCZ 11605 the lateral and ventrolateral stripes are indistinct (restricted to suture lines), and the snake is nearly plain brown. Specimens from farther south (RNP sample and Midongy du Sud) have varying degrees of black, sometimes extensive, on the venter and rows 1–2. In some RNP specimens, rows 1–2 are blackened so that only a central light spot of each scale remains (Fig. 21), whereas lateral stripes are rather distinct in most specimens from the RNP. In adults from Midongy du Sud (and one specimen from the RNP region, MCZ 180338), rows 1–3 (i.e., including the lateral stripe) and the adjacent venter are entirely blackened (Fig. 21); one near-hatchling (MCZ 180378; SVL 180 mm) from Midongy du Sud shows no general darkening of rows 1–3, suggesting that the black flanks in adults develop ontogenetically.

The extent of ventral pigmentation is highly variable within a locality. For example, in MCZ 180376 (Midongy du Sud) only the outer 12–15% of each ventral plate is black, with the rest of the venter immaculate whitish, whereas in MCZ 180379 from the same locality most of the ventral plates are obscured by black. Two specimens from a relatively high elevation in the RNP region (MCZ 180336–37, 1130 m) have relatively immaculate venters, whereas specimens from lower elevations in the same area (e.g., MCZ 180325–35, 850 m) have heavily pigmented venters. Günther (1882:265) commented that the venter was darker in females than in males, but that trend does not hold in the series from the Ranomafana region when other sources of variation are considered.

The Malagasy names *mandodrano* and *anakanify* are used for *Liopholidophis sexlineatus* in the RNP area.

*Liopholidophis pinguis* Parker  
 Figures 12, 22

*Liopholidophis pinguis* Parker, 1925:390 (Type locality: "Antsihanaka"). Holotype, BMNH 1946.1.7.66 (formerly 1925.8.25.7), an adult male [not seen]. Werner, 1929:11; Guibé, 1958:216; Dörmig, 1973:1397; Brygoo, 1983:55, 1987:24; UICN/PNUE/WWF, 1990:223; Glaw and Vences, 1992:266, 1994:338.

*Liopholidophis pinguis* Parker (1925) is not known to occur in the RNP. I have no field experience with the species and know nothing of its natural history.

**Holotype.** BMNH 1946.1.7.66 (not seen), an adult male obtained by W. F. H. Rosenberg; 890 mm total length, 300 mm tail length, with 151 ventrals and 91 subcaudals *vide* Parker (1925).

**Diagnosis.** A species of *Liopholidophis* having 17-17-15 dorsal scale rows, but lacking sexual dimorphism in tail length as extreme as in other members of the *sexlineatus* group. The number of midbody scale rows distinguishes *pinguis* (17) from members of the *stumpffi* group (19). The short tail (<35% total length) and corresponding low numbers of subcaudals (<110) in males distinguish *pinguis* from males of other members of the *sexlineatus* group (tail >35% total length and >120 subcaudals in males). *Liopholidophis pinguis* is most easily confused with *L. sexlineatus* (see "Key to Species"), and characters reliably separating females of the two species are subtle. The relative distinctness of the lateral stripes seems to be the most reliable feature (see "Key to Species" and species account for *sexlineatus*). Other species of the *sexlineatus* group have higher numbers of subcaudals (Table 1) and are either striped with distinctive nape spots (*rhadinæa*) or have distinctively patterned venters (*dolicocercus* and *grandidieri*) (see species accounts).

**Distribution.** Known from the vicinity of the type locality, Antsihanaka, and the nearby Lake Alaotra, and from the Perinet (=Andasibe) reserve (Appendix; Glaw and Vences, 1994:336 [map], 472); all are in the eastern forest region (Fig. 3). The locality for one specimen (SMF 61909) is recorded

as "Nord-Madagascar" (northern Madagascar), and the UICN/PNUE/WWF (1990) records "Moramanga" [18°56'S, 48°12'E] without documentation. See "Remarks."

**Description.** The following description is based on examination of 6 females and 5 males but incorporates data for the holotype (Parker, 1925). Measurements, proportions, and scutellation are summarized in Table 1. Largest specimen the male holotype (BMNH 1946.1.7.66), 890 mm total length, 300 mm tail length (34% of total; Parker, 1925); largest female (BMNH 1936.3.3.94-97, largest of two females in the series), 664+ mm total length, incomplete tail 86+ mm. Proportional tail length moderately sexually dimorphic, 30-34% of total length in males, 25-26% in females. Dorsal scales smooth, lacking apical pits, in 17-17-15 rows. Scale row reduction from 17 to 15 rows by loss of row 4 (N = 6 sides), fusion of 3 + 4 (N = 4 sides), or fusion of 4 + 5 (N = 4 sides) at the level of ventrals 87-102. Ventrals 147-154 in males, 139-147 in females. Anal plate divided. Subcaudals 88-99 in males, 67-71 in females. Eight upper labials with 4-5 touching eye (unilateral presence of 9 in one specimen). Lower labials 10-10 (N = 5) or 9-10 (N = 5), the first pair in contact behind the mental, 1-4 or 1-5 touching an anterior genial, 4-5 or 5-6 touching a posterior genial. Anterior genials shorter than posterior genials. Loreal present. Preocular usually single (unilaterally divided in two specimens). Postoculars 2. Temporals 1 + 2.

Body about as high as, or slightly higher than, wide; ventrolateral edge of body slightly angulate. Head slightly wider than neck. Pupil round. Eye very small, its diameter less than the distance between the eye and posterior edge of nostril ( $\bar{x}$  = 0.88 ± 0.06; range 0.77-0.94; N = 5). Scattered pits on head plates.

**Dentition.** Maxillary teeth 20-24 + 2 (N = 9;  $\bar{x}$  = 21.7 ± 1.3 prefang teeth). Diastema absent; gap <1 tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row,

twice as large as the posteriormost maxillary teeth; having a rounded anterior surface (except for distal portion, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed. A skull (MCZ 11701, male) has 13–13 palatine teeth, 28–30 pterygoid teeth, and 29–28 dentary teeth.

*Hemipenis.* Deeply bilobed (somewhat less than half total length), noncapitate, acalyculate (entirely spinose), with a deeply bifurcate centrolateral sulcus spermaticus.

*Coloration in Preservative (Based on USNM 149242 and SMF 61909; AMNH 60692 is similar; see Fig. 22).* These are the most recently collected and best-preserved specimens I have seen. No distinct stripes on most of the body, but thin darkened edges to many dorsal scales gives a somewhat braided appearance. Dorsal ground color grayish brown. Thin dark postocular bar extending from extreme lower edge of lower postocular and upper edge of supralabial 5, across lower edge of anterior temporal/upper edge of labials 6–7, ending on anterior portion of labial 8. Except for thin upper blackened border, supralabials dirty white finely peppered with dark. Minute tubercles and pits on anterior head plates. Blackened suture line between ventrals and dorsal row 1, broadening on posterior body and tail to form a distinct stripe at subcaudal/dorsal caudal suture that continues to the tail tip. Similar blackened border between rows 2 and 3 on posterior  $\frac{1}{2}$  of body (ending at vent or on anterior part of tail), forming a distinct stripe on posterior 30% of body in SMF 61909. Scale row 3 of SMF 61909 highlighted with white dots on anterolateral portion of each scale (more evident anterior to lateral stripe and dots more consistently present on upper edge of scales); similar, but less distinct, dots present in USNM 149242.

Venter grayish white with most ventrals (especially posteriorly) having thin blackened anterior border. Subcaudals immaculate grayish white, except for the lateral blackened edge.

A series of *Liopholidophis pinguis* from "Lake Alaotra" (BMNH 1936.3.3.94–97) and another series probably from close to there (MCZ 11698–701; see Appendix for comment) are similar to those just described but have more distinct lateral stripes. The stripe along the suture between the ventrals and dorsal row 1, manifested by black pigment at the extreme lateral edges of the ventrals, is obvious primarily on the posterior body and on the tail. A lateral stripe is manifested by a series of dashes or small dots on row 3 anteriorly (pigment at anterior–posterior junction of adjacent scales), or on the suture between rows 2 and 3 posteriorly; anteriorly, it is invariably a "dotted" line; posteriorly, it varies from bare shading of the suture line in a zigzag pattern to a distinct lateral stripe involving more of the adjacent scales. The lateral stripe either stops at the vent or on the anterior part of the tail or merges with the ventrolateral stripe; tail with a black stripe at lateral edges of the subcaudals continuous with the ventrolateral body stripe. In the MCZ series, dorsal row 3 on the anterior  $\frac{1}{2}$ – $\frac{2}{3}$  of the body is highlighted by a pair of white dashes on the anterolateral portions of each scale; row 7 is partially similarly highlighted in one specimen. The venter is either immaculate, has obscure irregular grayish markings, or has suture lines between adjacent ventrals outlined indistinctly in black. Two specimens have a series of irregular dashes laterally on each ventral (distinct only anteriorly in one of the two). The supralabials are largely immaculate; a dark postocular bar extends across the top of the last 3 supralabials from the ventroposterior edge of the eye. The gular region and infralabials are immaculate.

Parker (1925) reported the type as having a distinct black lateral stripe from the eye to the vent on scale row 3 (2 + 3 posteriorly), black spots on the outer ends of the ventrals and subcaudals, and a series of indistinct black dots on either side of the midventral line.

*Remarks.* The type locality, Antsihan-



Figure 22. *Liopholidophis pinguis* Parker. Specimen (USNM 149242) from Perinet [=Andasibe]. See also Figure 12.

aka, is the name for a region in the vicinity of Lake Alaotra, a large freshwater lake at the edge of the central plateau. The Sihanaka are one of Madagascar's indigenous peoples inhabiting the area around the lake; "Antsihanaka" literally means "land of the Sihanakas." See, for example, the maps of indigenous peoples in Gallieni (1908:pl. 6) and Grandidier (1893). *Sihanaka* can also mean simply "lake," from which the name of the people and the region may derive. The locality was discussed by Carleton and Schmidt (1990:9) as "Sihanaka Forest." Parker (1925:390) stated that the Antsihanaka country was "situated between Lake Alaotra and the first belts of the eastern forest."

A series of *pinguis* in the MCZ from the "eastern Forest" was heretofore identified as *sexlineatus* (MCZ 11698-701 collected by Frederick R. Wulsin, June to September, 1915). According to Barbour (1918:479), the portion of Wulsin's collection labeled as coming from the "Eastern Forest" was collected "at a point about half way between Tamatave and Tananarive" (=Toamasina and Antananarivo, respectively). Unfortunately, the data are no more precise. Wulsin collected at Andaingo

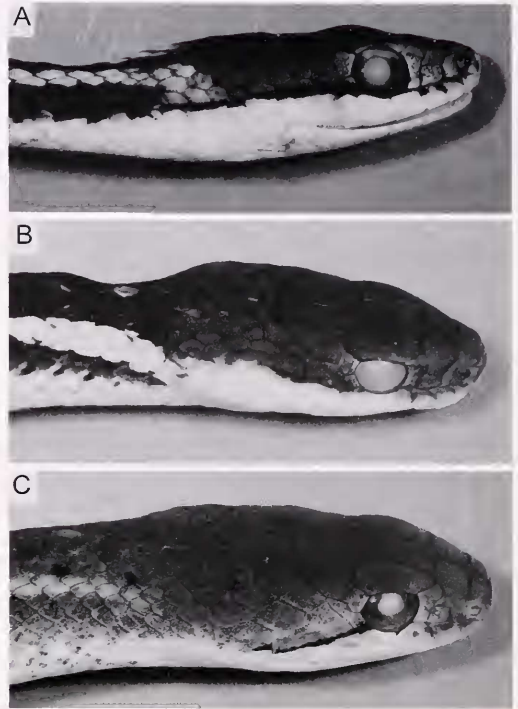


Figure 23. Heads of species of the *Liopholidophis stumpffi* group, in dorsolateral view. A. *L. epistibes*, new species (MCZ 180324). B. *L. lateralis* (Duméril, Bibron, and Duméril) (MCZ 180349). C. *L. infrasignatus* (Günther) (MCZ 180359). See Figures 8 and 25 for *L. stumpffi* (Boettger) and also Figure 28 for *L. infrasignatus* (Günther).

(18°12'S, 48°17'E; Barbour, 1918:478), just south of Lake Alaotra, from where most specimens of *pinguis*, including the type, seem to have come. Wulsin's specimens of *pinguis* could be from this region, whose location is consistent with Barbour's more vague description of the locality.

#### The *stumpffi* Species Group (Parker, 1925)

Figures 23-29 (see also Figs. 7-11);  
Table 2

**Content.** *Dromicus stumpffi* Boettger, 1881a:358, 1881b:441.

*Leptophis lateralis* Duméril, Bibron, and Duméril, 1854:544.

*Ptyas infrasignatus* Günther, 1882:263. (Senior synonym of *Liopholidophis thieli* Domergue, 1973, of recent authors, as shown later).

*Liopholidophis epistibes*, described herein.

The *stumpffi* group includes two broadly distributed species, *infrasignatus* and *lateralis*, and I have not undertaken a study of their geographic variation. A more thorough investigation may show these to be composites.

*Liopholidophis stumpffi*  
(Boettger)

Figures 8, 24–25

*Leptophis lateralis* Duméril, Bibron, and Duméril, 1854 (part): (Type locality, Madagascar). Syntypes, MNHN 7312 (1 ♂, 3 ♀) *vide* Guibé (1958:214) [not seen]. Günther, 1890:70. Boulenger, 1893:247. Mocquard, 1904:302.<sup>10</sup>

*Thamnosophis lateralis* Jan and Sordelli, 1879: Boulenger, 1893:247.

*Dromicus stumpffi* Boettger, 1881a:358, 1881b:441, pl. 1, fig. 2 (Type locality, Nossi-Bé). Syntypes: three specimens collected by Antonio Stumpff and originally in the Senckenberg Museum; presumably three of four adults listed under catalog number 7247a by Boettger (1898:25). SMF 17576 is here designated the lectotype; see remarks.

*Ptyas infrasignatus* Günther, 1882: Günther, 1890: 70 (synonym of *Dromicus stumpffi* Boettger). Boulenger, 1893:247 (synonym of *Tropidonotus stumpffi*). *Ptyas infrasignatus* is here recognized as a valid senior synonym of *Liopholidophis thieli* Domergue, 1973 (see later).

*Dromicus baroni* Boulenger, 1888:104: (Type locality, Madagascar). Holotype, BMNH 1946.1.7.67 (old number 87.12.22.38) [examined]. Günther, 1890:70 (synonym of *Dromicus stumpffi* Boettger). Boulenger, 1893:247 (synonym of *Tropidonotus stumpffi*). Here recognized as a synonym of the resurrected *Ptyas infrasignatus* Günther.

*Tropidonotus stumpffi* (Boettger): Boulenger, 1893: 247. Boettger, 1898:25, 1913:312; Mocquard, 1895a: 102, 1895b (*Tropidonotus stumpfei*); Jourdan, 1903:32 (*T. stumpfi*). Boulenger, 1915:373–374. Kaudern, 1922:445 (cited specimen probably = *L. epistibes*; see species account).

<sup>10</sup> *Liopholidophis lateralis* has, since Boulenger (1893), been assigned to the synonymy, in part, of *stumpffi* Boettger. But the general confusion of *stumpffi*, *epistibes*, and *infrasignatus* in the literature suggests a reevaluation. Guibé (1954:242) gave 166 as the ventral count for the male syntype of *lateralis* and stated that it has “a median black spot on each ventral” (Guibé, 1958:214). Both statements conform more to *epistibes* than to other members of the *stumpffi* group (see Table 2 and other species accounts). Nonetheless, the syntypes of *lateralis* must be reexamined to correctly place the synonymy.

*Liophidium gracile* Mocquard, 1908:261: (Type locality, Montagne d’Ambre and Nossi-Bé). Syntypes, MNHN 1893.211, an adult male collected May–July, 1893 by Alluaud and Belly at Montagne d’Ambre (Mocquard, 1895:123) [examined]; and MNHN 84-595, a juvenile, probably female, collected at Nossi-Bé [examined]. Boulenger, 1915:374 (questionably listed as synonym of *Tropidonotus stumpffi*). Both of the syntypes of *Liophidium gracile* are here recognized as the same taxon as *Dromicus stumpffi* Boettger.

*Liopholidophis lateralis* (Duméril, Bibron, and Duméril) (part): Mocquard, 1909:89; Werner, 1929: 11; Guibé, 1954:243, 1958:213. (*Dromicus stumpffi* Boettger listed as synonym).

*Liopholidophis stumpffi* (Boettger): Parker, 1925:391. Domergue, 1973:1401; Nicoll and Langrand, 1989: 44, 72, 130; Brygoo, 1983:55, 1987:24; UICN/PNUE/WWF, 1990:223; Glaw and Vences, 1992: 226, 1994:338. As noted in the description of *L. epistibes* herein, most of Domergue’s (1973) specimens of “*stumpffi*” from eastern Madagascar (followed by subsequent authors) probably are *epistibes*.

*Liopholidophis infrasignatus* (Günther): Parker, 1925: 391 (synonym of [*Dromicus*] *stumpffi* Boettger).

*Notes on Types and Designation of Lectotype.* Boettger (1881a,b) described *Liopholidophis stumpffi* from three specimens collected by Antonio Stumpff, consul to Madagascar, on the island of Nosy-Be (the former paper is a brief description in Latin; the latter paper repeats verbatim the Latin description, followed by a detailed description in German). Boettger (1881b) gave detailed measurements and scale counts for the three syntypes. I examined eight specimens collected by Stumpff at the type locality (BMNH 1946.1.23.51, FMNH 18291, SMF 17576 [listed as “*typus*” in SMF records], SMF 17580-84). With the exception of SMF 17576, my scale counts and measurements do not correspond well with the details given by Boettger (1881b), and SMF 17576 (Figs. 24–25) is hereby designated the lectotype of *Dromicus stumpffi* Boettger.

SMF 17576 apparently is specimen “No. 1” in Boettger (1881b). Details on this specimen are as follows (Boettger’s data in parentheses): A gravid adult female, total length 711 mm (750), tail length 236 mm (237), tail as a proportion of total length 33%; 2 preventrals + 151 ventrals (153),



TABLE 2. VARIATION IN MENSURAL AND MERISTIC CHARACTERISTICS OF SPECIES OF THE *LIOPHOLIDOPHIS STUMPFII* GROUP. SCALE COUNTS AND BODY PROPORTIONS ARE  $\bar{x} \pm SD$  (SAMPLE SIZE) WITH RANGES BELOW IN PARENTHESES; MAXILLARY TOOTH COUNTS ARE PREFANG COUNT RANGES (+2 FANGS), FOLLOWED BY  $\bar{x} \pm SD$  (SAMPLE SIZE). TABULATIONS FOR *INFRASIGNATUS* INCLUDE DATA ON VENTRAL AND SUBCAUDAL COUNTS AND RELATIVE TAIL PROPORTIONS OF *L. THIELI* FROM TABLE II OF DOMERGUE (1973:1405).

	<i>stumpffi</i>	<i>epistibes</i> <sup>1</sup>	<i>lateralis</i>	<i>infrassignatus</i>
Dorsals	19-19-17	19-19-17	19-19-17	19-19-17
Ventrals				
Males	150.7 ± 1.37 (6) (149-153)	162.3 ± 3.55 (7) (157-166)	154.0 ± 4.83 (28) 144-165 <sup>2</sup>	149.0 ± 3.18 (17) (141-156)
Females	149.4 ± 4.02 (7) (145-157)	160.6 ± 4.63 (17) (151-167)	159.5 ± 4.86 (20) 151-166	152.7 ± 3.86 (35) (144-161)
Subcaudals				
Males	97.0 ± 6.00 (6) (89-104)	96.7 ± 4.35 (7) (91-104)	89.5 ± 6.26 (22) (80-98)	73.4 ± 4.27 (15) (66-81)
Females	98.3 ± 5.47 (7) (91-109)	88.8 ± 3.53 (16) (83-96)	87.9 ± 6.31 (15) (76-97)	67.7 ± 2.64 (30) (62-73)
Maximum length (mm)				
Total (SVL)				
Males	627 (416)	709 (471)	729 (517)	727+ (606)
Females	711 (475)	829+ (634)	820 (586)	920 (712)
Tail length/total				
Males	0.32 ± 0.02 (6) 0.29-0.34	0.31 ± 0.02 (7) 0.28-0.34	0.29 ± 0.01 (22) 0.27-0.31	0.25 ± 0.01 (16) 0.23-0.27
Females	0.33 ± 0.01 (7) 0.31-0.34	0.29 ± 0.01 (15) 0.27-0.31	0.27 ± 0.01 (15) 0.25-0.29	0.23 ± 0.01 (29) 0.21-0.24
Maxillary teeth	25 + 2-31 + 2 27.8 + 2 (6)	22 + 2-29 + 2 26.4 + 2 (16)	25 + 2-30 + 2 26.6 + 2 (18)	20 + 2-25 + 2 22.3 + 2 (28)
Eye diameter/eye-nostril distance	1.22 ± 0.07 1.13-1.31 (7)	1.38 ± 0.17 1.16-1.69 (12)	1.1 ± 0.09 0.97-1.3 (24)	1.21 ± 0.10 1.06-1.44 (19)

<sup>1</sup> As noted in the text, most specimens referred to *L. stumpffi* by Domergue (1973:table I) probably are *epistibes*. Extreme values for meristic and mensural statistics represented by Domergue's specimens, where different from those reported here, are ventrals: ♂, 151; subcaudals: ♂, 105; ♀, 80; total length: ♂, 798 (548); ♀, 945 (675); tail length/total: ♀, 0.32. In these I have excluded Domergue's specimen from Marojezy, which may represent true *stumpffi* (see text, "Distribution" in the *epistibes* species account).

<sup>2</sup> Domergue (1972:table III) reported the following ranges for meristic counts for *lateralis*: ventrals 154-170 (♂), 152-174 (♀); subcaudals 86-99 (♂), 58-98 (♀). I suspect low values for the female subcaudal counts reflect incomplete tails. As Domergue did not give values for individual specimens, these data were not included in calculations provided here.

divided anal plate, subcaudals 96 (98), 1 preocular, 2 postoculars, 2 + 2 temporals; 8-8 supralabials, 4-5 in contact with eye; 10-10 infralabials. Dorsals in 19-19-17 rows, the posterior reduction occurring by fusion of rows 3 + 4 at the level of ventrals 92-90. Horizontal eye diameter 4.0 mm. Anterior edge of eye to posterior edge of nostril 3.1 mm.

*Diagnosis.* *Liopholidophis stumpffii* differs from members of the *sexlineatus* group

in having 19-19-17 dorsal scale rows (vs. 17-17-15). It differs from other species of the *stumpffi* group primarily in color pattern and a few body proportions, including the following: relatively long tail and high number of subcaudals (31-34% of total length and 91-109, respectively, sexes combined); dorsolateral light stripe on rows 4-5 on neck and anterior part of body, row 4 or 4-5 when present posteriorly; dark postocular stripe separated from dark

blotches on side of neck; dorsolateral light stripe continuous with light color of throat; venter mostly immaculate except for pigment encroaching laterally from flanks (small spots may be present on extreme anterolateral edge of anterior ventral plates, but these are not inset from edge of the plates).

*Liopholidophis stumpffi* is most easily confused with *epistibes*, and their distinguishing characteristics are given in the account for the latter.

*Liopholidophis stumpffi* differs from *L. lateralis* in the position of the lateral stripes: in *stumpffi* on dorsal rows 4–5 on neck and anterior body, usually fading posteriorly (indistinct on tail); in *lateralis* on rows 3–5 (occasionally only row 4), very distinct the length of the body, continuing to the tail tip. The species also differ in color pattern: indiscrete dark spots on neck and anterior body, and brownish posterior body with light stripes indistinct or absent in *stumpffi*; continuous dark middorsal stripe and flanks, separated by vivid light stripes the length of the body in *lateralis*.

*Liopholidophis stumpffi* differs from *infrassignatus* in the orientation of the postocular dark bar. In *stumpffi* the bar extends horizontally posterior to the eye, paralleling the upper border of the posterior supralabials (Figs. 8, 25); in *infrassignatus* the bar extends at an angle downward across the penultimate and ultimate supralabials (Figs. 23, 28). In *stumpffi* the dorsolateral light stripe anterior is on scale rows 4–5 (5–6 in *infrassignatus*). *Liopholidophis stumpffi* also has a longer tail than *infrassignatus* (31–34% of total length vs. 21–27%, sexes combined; see Table 2), is of more gracile habitus, and has more distinct spots on the neck (present or not in *infrassignatus*, but not conspicuous).

*Distribution.* *Liopholidophis stumpffi* is here considered a species of extreme northern Madagascar. Most specimens examined are from the island of Nosy-bé, the type locality; three specimens (including one syntype of *Liophidium gracile* Mocquard) are from near the northern tip of mainland Madagascar in the vicinity of

Montagne d'Ambre (Fig. 6 and Appendix). As pointed out in the account for *Liopholidophis epistibes*, most literature records of "*stumpffi*" from eastern Madagascar probably represent *epistibes*, and the distributional relationships between the two species in northern Madagascar are unclear.

*Description.* The following description is based on examination of seven females and six males, including the lectotype and other topotypical material (see preceding comments) of *Dromicus stumpffi* Boettger and the two syntypes of *Liophidium gracile* (Mocquard). Measurements, proportions, and scutellation are summarized in Table 2. Largest specimen a female, 711 mm total length, tail 236 mm; largest male 627 mm total length, 211 mm tail length. Tail length not sexually dimorphic, 32–34% of total length in males, 31–33% in females. Dorsal scales smooth, in 19–19–17 rows; 0–2 apical pits on different scales within an individual. Five of seven specimens showed posterior scale reduction by fusion of rows 3 + 4 at the level of ventrals 84–95; two of six specimens from the type locality for which this character was determined had fusion of rows 4 + 5 at ventrals 92–93.<sup>11</sup> Ventrals 149–153 in males, 145–157 in females. Anal plate divided. Subcaudals 96–104 in males, 91–109 in females. Eight upper labials (rarely seven or nine) with 4–5 touching eye. Lower labials usually 10–10 (eight specimens), with 9–10 (1) and 10–11 (1) being uncommon variants; first pair in contact behind the mental, 1–5 touching an anterior genial, 5–6 touching a posterior genial. Anterior genials shorter than posterior genials. Loreal present. Preocular single. Temporals 2 + 2.

Body slightly higher than wide; ventrolateral edge of body slightly angulate. Head

<sup>11</sup> The type locality is an island, and the high frequency of an "unusual" scale reduction pattern (fusion of 3 + 4 seems to be the common mode of reduction in *Liopholidophis*) could reflect the isolated nature of the population. No other scale anomalies were detected in these specimens.

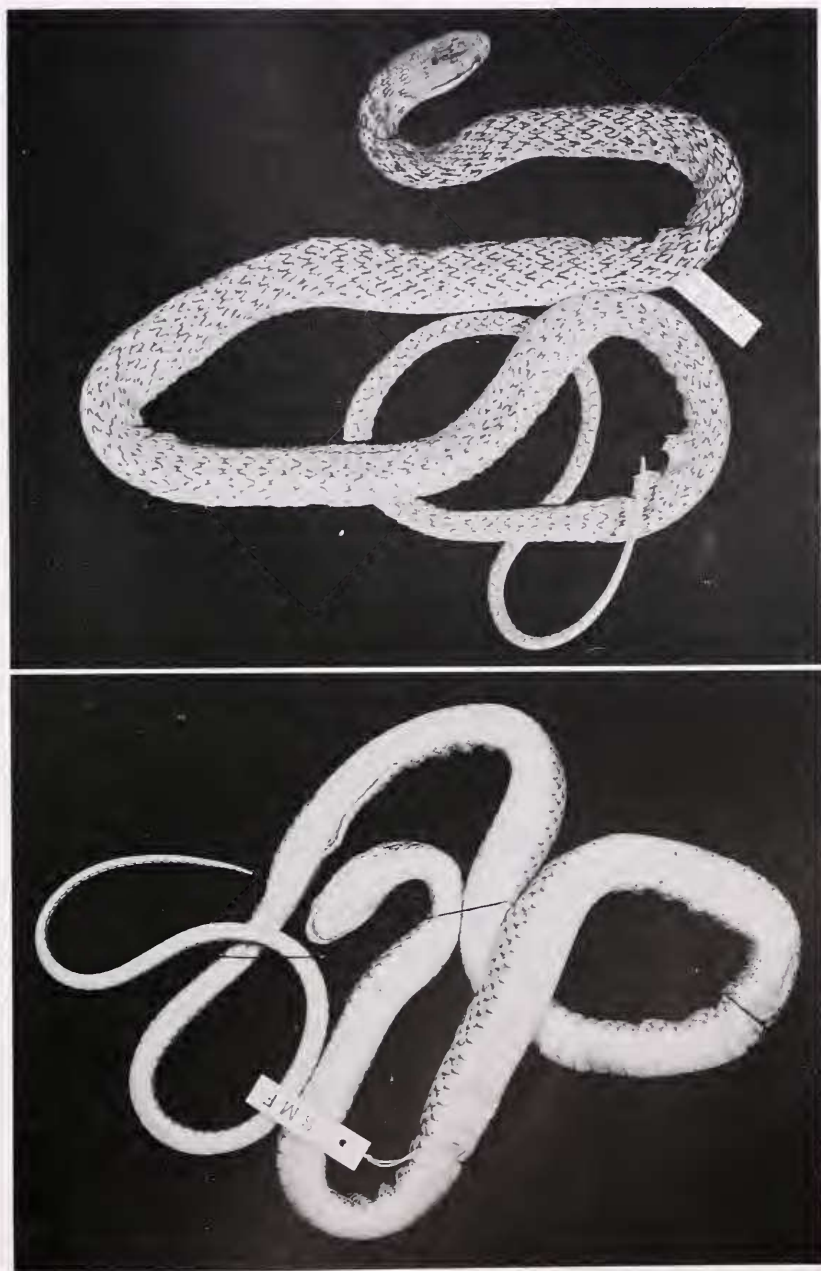


Figure 24. *Liopholidophis stumpffi* (Boettger), lectotype (SMF 17576, female) from "Nossi-Bé." Dorsal and ventral views.

slightly wider than neck. Pupil round. Eye large (Figs. 8, 23, 25), its diameter greater than the distance between eye and posterior edge of nostril ( $\bar{x} = 1.22 \pm 0.07$ ;

range 1.15–1.31;  $N = 7$ ). Scattered minute pits on head plates, especially the supraoculars, prefrontals, and nasals.

*Dentition.* Maxillary teeth 25–31 + 2

( $N = 6$ ;  $\bar{x} = 27.8 \pm 2.23$  prefang teeth). Diastema absent; gap  $< 1$  tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row, 2 times as large as the posteriormost maxillary teeth; having a rounded anterior surface (except for distal portion, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed.

*Hemipenis.* Very deeply bilobed (dividing at the base of the organ and having an extremely short stalk), acalyculate (entirely spinose), and with a deeply divided centrolineal sulcus spermaticus. Tips of the lobes with a central "umbelliform" depression.

*Coloration in Life.* Unknown.

*Coloration in Preservative.* Most specimens I studied had lost most of the stratum corneum, and appear grayish with a black network the length of the body (formed by black borders to many scale rows), black irregular spots on the neck, and dorsolateral light stripes that vary in extent and discreteness. Two adult topotypes (FMNH 18291, SMF 17581) retain the stratum corneum. These are more or less brown snakes with an indistinct dark network on the dorsal scales, indistinct dark spots on the neck (generally 2–4 dorsal scales in size), and indistinct dorsolateral light stripes; top of the head brown to grayish brown; supralabials, infralabials, and gular region dirty whitish; blackish postocular bar; venter yellowish white, with dark encroaching pigment from flanks on lateral edges of ventral scales (plus dark punctations at lateral edges of anterior ventrals, as described in the diagnosis). The dorsolateral light stripes are anteriorly confluent with light color of the throat (Figs. 8, 25); they occupy rows 4–5 anteriorly, usually fading by midbody but on rows 4 or 4–5 when present posteriorly. In several individuals, including juveniles and adults (e.g., MCZ 54368, MNHN 1893-211), the light stripes continue to the tail tip and are bordered ventrally at the subcaudal/dorsal caudal suture by a blackish streak.

Three small juveniles (SMF 17582–84; total lengths 195–308 mm) are similar to adults in pattern, and the dorsolateral stripes also vary in discreteness and length, as in adults.

*Natural History.* *Liopholidophis stumpffi* presumably is diurnal and terrestrial like other members of the *stumpffi* group.

The lectotype (SMF 17576; SVL 475 mm; month of collection unknown) is a gravid female with four large eggs, as determined by palpation.

*Remarks.* The FMNH and the BMNH have specimens of *Liopholidophis stumpffi* collected by Stumpff on Nosy-Be and exchanged with the Senckenberg Museum in the 1880s (FMNH 18291 and BMNH 1946.1.23.51, respectively). The FMNH records indicate their specimen as a "paratype" (see, e.g., Marx, 1958:480), an impossible designation because Boettger's series consisted of three syntypes. Boulenger (1893:247) noted the BMNH specimen "As typical of *D. stumpffi*"; such a designation would be unlikely if the BMNH specimen were really a syntype, because in such cases Boulenger routinely used the word "type." In any case, my measurements and scale counts for these specimens do not correspond to any of the three syntypes of *stumpffi*, as reported by Boettger (1881a). Boettger (1898:25) listed eight specimens (catalog number 7247a) from Nosy-Be collected by Stumpff in the Senckenberg Museum at that time. In addition to the FMNH and BMNH specimens, the SMF now has several specimens collected by Stumpff on Nosy Be (Appendix).

Boettger (1881a,b) stated that *Liopholidophis stumpffi* has "two distinct apical pits." My observations revealed that the number of apical pits varies from 0 to 2 within an individual, even considering only those scale rows that occasionally had pits.

*Liopholidophis lateralis*  
(Duméril, Bibron, and Duméril)  
Figures 23, 26

*Leptophis lateralis* Duméril, Bibron, and Duméril, 1854:544, part (Type locality, "Madagascar").



Figure 25. *Liopholidophis stumpffi* (Boettger), lectotype (SMF 17576, female). Dorsolateral view of head.

*Dromicus melanotus*, var. ? Günther, 1858:133; Boulenger, 1893:248 (synonym of *Tropidonotus lateralis*).

*Thamnosophis lateralis* (Duméril, Bibron, and Duméril): Jan, 1863:133. Jan and Sordelli, 1879:liv. 49, pl. II. Boulenger, 1893:248 (synonym of *Tropidonotus lateralis*). Guibé, 1954:243, 1958:213 (synonym of *Liopholidophis lateralis*).

*Dromicus madagascariensis* Günther, 1872:22, pl. V, fig. A.: (Type locality, "Madagascar"). Syntypes, BMNH 1946.1.15.19 (female), collector unknown, and BMNH 71.6.28.17 (male), obtained by Mr. Bar-

lett [both examined]. The latter specimen is here recognized as the male syntype upon which Günther based his description. Boulenger, 1893:248 (synonym of *Tropidonotus lateralis*). Guibé, 1954:243, 1958:213 (synonym of *Liopholidophis lateralis*).

*Ahaetulla lateralis* (Duméril, Bibron, and Duméril): Boettger, 1877:33. Boulenger, 1893:248 (synonym of *Tropidonotus lateralis*). Guibé, 1954:243, 1958:213 (synonym of *Liopholidophis lateralis*).

*Philothamnus lateralis* (Duméril, Bibron, and Duméril): Boettger, 1881b:526. Boulenger, 1893:248 (synonym of *Tropidonotus lateralis*). Guibé 1954:243, 1958:213 (synonym of *Liopholidophis lateralis*).

*Dromicus stumpffi* Boettger, 1881a:358, 1881b:441, pl. 1, fig. 2; Mocquard, 1904:302, 1909:89; Guibé, 1954:243, 1958:213. (synonym of *Liopholidophis lateralis*). Here considered a valid taxon.

*Ptyas infrasignatus* Günther, 1882; Guibé, 1954:243, 1958:213 (synonym of *Liopholidophis lateralis*). Here recognized as a valid taxon.

*Dromicus baroni* Boulenger, 1888:104; Guibé, 1954:243, 1958:213 (synonym of *Liopholidophis lateralis*). Here considered a synonym of the resurrected *Liopholidophis infrasignatus* (Günther).

*Tropidonotus lateralis* (Duméril, Bibron, and Duméril): Boulenger, 1893:248, 1915:374. Boettger, 1898:25, 1913:312. Jourdran, 1903:32. Kaudern, 1922:444.



Figure 26. *Liopholidophis lateralis* (Duméril, Bibron, and Duméril). Specimen from the RNP, MCZ 180353.

*Liopholidophis lateralis* (Duméril, Bibron, and Duméril): Mocquard, 1904:303, 1909:43; Parker, 1925:391; Werner, 1929:11; Guibé, 1954:243, 1958:213; Domergue, 1973:1398; Brygoo, 1983:55, 1987:24; Nicoll and Langrand, 1989:48, 88; UICN/PNUE/WWF, 1990:223; Glaw and Vences, 1992:266, 1994:337.

*Liophidium gracile* Mocquard, 1908:261: (Type locality, Montagne d'Ambre and Nossi-Bé). Syntypes, MNHN 1893.211 and MNHN 84-595 (see synonymy of *Liopholidophis stumpffi* Boettger for data). Guibé, 1958:213 (synonym of *Liopholidophis lateralis*). Here considered a synonym of *Dromicus stumpffi* Boettger.

**Syntypes.** MNHN 7312 (1 ♂, 3 ♀) *vide* Guibé (1958:214) [not seen]. Guibé (1954, 1958) gave some meristic counts and other descriptive data on the types.

**Diagnosis.** *Liopholidophis lateralis* differs from members of the *sexlineatus* group in having 19-19-17 dorsal scale rows (vs. 17-17-15). It is the only species of *Liopholidophis* with vivid dorsolateral light stripes (white to yellowish in life) centered on row 4 the entire length of the body and tail (adjacent parts of rows 3 and 5 usually also involved) (Fig. 26; Glaw and Vences, 1994:pl. 346). The dorsolateral light stripes are on rows 5-6 or 5-7 anteriorly in *epistibes* and *infrasinatus* and are indistinct posteriorly in *stumpffi* (see species account for other differences).

Superficially, *Liopholidophis lateralis* is similar to *Dromicodryas bernieri*. These two species can be distinguished in life by the brown (vs. black) dorsal ground color of *D. bernieri* as compared to *lateralis* (compare Glaw and Vences, 1994:pls. 342, 346) and by the anterior disposition of the dorsolateral light stripe: confluent or nearly so with the light gular coloration in *L. lateralis*, separated by dark flank coloration in *D. bernieri* (cf. Glaw and Vences, 1994:figs. 505-507). *Dromicodryas* has enlarged anterior mandibular teeth and differs in fundamental hemipenial characteristics from *Liopholidophis* (Guibé, 1958; personal observations).

**Distribution.** *Liopholidophis lateralis*, as presently understood, has an extraordinary geographic and macroenvironmen-

tal range, including the eastern lowlands and montane rainforest belt, scattered localities on the central plateau, and dry forests of western Madagascar (Fig. 6; for more comprehensive distribution maps, see Glaw and Vences, 1994:336; Domergue, 1973:1398). Domergue (1973:1401) recorded localities from sea level to more than 2,000 m elevation. Such an ecological amplitude for a snake species is rare and warrants a thorough assessment of geographic variation. In the vicinity of the RNP, *Liopholidophis lateralis* is known from approximately 500 to 900 m elevation.

**Description.** The following description is based on examination of 20 females and 28 males. Measurements, proportions, and scutellation are summarized in Table 2. Largest specimen a female (MCZ 11663), 820 mm total length, 234 mm tail length (29% of total); largest male (MCZ 180345) 729 mm total length, 212 mm tail length (29% of total; tip of tail missing). Tail length not strongly sexually dimorphic, 27-31% of total length in males, 25-29% in females. Dorsal scales smooth, in 19-19-17 rows (one individual each with 21-19-17 and 17-19-17); usually two apical pits on scales of all rows between the dorsolateral stripes (see "Remarks"). Scale row reduction from 19 to 17 rows by fusion of rows 3 + 4 (occasionally appears as loss of row 4) at the level of ventrals 85-105 (N = 11; two specimens with unilateral fusion of 4 + 5). Ventrals 144-165 in males, 151-166 in females. Anal plate divided. Subcaudals 80-97 in males, 76-97 in females. Eight upper labials with 4-5 touching eye. Lower labials usually 10-10 (N = 19), other variants being 8-9 (2), 9-9 (5), 9-10 (12), and 10-11 (4), the first pair in contact behind the mental, 1-5 (rarely 1-6) touching an anterior genial, 5-6 (rarely 6-7) touching a posterior genial. Anterior genials shorter than posterior genials. Loreal present. Preocular single. Temporals usually 2 + 2 (occasionally 1 anterior temporal or, less frequently, 1 posterior temporal; rather high frequency of azygous temporal

scales, fragmentation of scales in temporal region, or fusion of a temporal with a supralabial).

Body slightly higher than wide; ventrolateral edge of body slightly angulate. Head distinctly wider than neck. Pupil round. Eye moderately large, its diameter equal to or slightly greater than the distance between the eye and posterior edge of nostril ( $\bar{x} = 1.1 \pm 0.09$ ; range 0.97–1.30;  $N = 24$ ). Scattered pits and tubercles on circumorbital and anterior head plates.

**Dentition.** Maxillary teeth 25–30 + 2 ( $N = 17$ ;  $\bar{x} = 26.6 \pm 1.6$  prefang teeth). Diastema absent; gap <1 tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row, twice as large as the posteriormost maxillary teeth; having a rounded anterior surface (except for distal portion, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed. Two skulls, MCZ 180350 and AMNH 60676 (both females) have the following tooth counts, respectively: 16–?, ?–21 palatine teeth; ?–35, 31+–34 pterygoid teeth; 30–31, ?–34 dentary teeth.

Domergue (1973) reported 13–15 maxillary teeth and 15–23 dentary teeth in *Liopholidophis lateralis*, about half the tooth number I counted (25–30 prefang maxillary teeth and 30+ dentary teeth); I assume that Domergue failed to count empty sockets.

**Hemipenis** (Fig. 35). Deeply bilobed, noncapitate, acalyculate (entirely spinose), with a deeply bifurcate centrolineal sulcus spermaticus. Sulcus spermaticus centrolineal, dividing near the base of the organ. Tips of the lobes with a central “umbelliform” depression.

**Coloration in Life and Preservative.** In life, *Liopholidophis lateralis* appears as a black snake with whitish to yellowish lateral stripes (see Glaw and Vences, 1994: pl. 306). The lateral light stripes usually occupy row 4 and adjacent halves of rows 3 and 5 (occasionally rows 4–5, and in MCZ 180345 essentially restricted to row 4 an-

teriorly, 3–4 posteriorly); the stripes are continuous from the nape to the tip of the tail (uninterrupted at vent). Anteriorly, the stripes are usually confluent with the light (yellowish to whitish) color of the throat (occasionally separated by a narrow line of dark pigment; see Glaw and Vences, 1994:fig. 505). Dorsal rows below the lateral stripe are blackish, except for row 1, which tends to have only a stippling of blackish pigment (appears dirty white to grayish). The venter and underside of the tail are immaculate whitish to pale yellow, usually with outer edges of ventrals stippled with dark pigment and/or with small rounded black dots.

In preservative, the light stripes are whitish and the dorsal ground color grayish black to brownish. Upon loss of the stratum corneum, the scales become grayish or grayish brown.

**Natural History.** *Liopholidophis lateralis* is diurnal and terrestrial. It occurs in relatively open, often disturbed, areas (secondary growth and rice fields). I have never observed it in closed-canopy forest, either primary or moderately dense secondary forest. Domergue (1973:1401) and Glaw and Vences (1994:337) reported *L. lateralis* as being semiaquatic, but other than occasional (and, in Madagascar, inevitable) association with flooded rice fields, this species in my experience does not appear to be especially associated with water, certainly not to the extent of *L. sexlineatus*. *Liopholidophis lateralis* is abundant in appropriate open microhabitats in the vicinity of the RNP and seems especially active on very hot days.

These snakes often raise the head and anterior  $\frac{1}{3}$  of the body off the ground as an intruder approaches. They bite rather ineffectively (small teeth) when captured and often flatten the neck and body for about  $\frac{2}{3}$  of its length, exposing white skin between scales and broadening the body stripes. Domergue (1973:1401) also reported body inflation and neck flattening in *Liopholidophis lateralis*, exposing white markings on the scales. One individual I

observed extended the tongue while slowly flicking it up and down, or held the tongue extended with little movement except at the tips for extended periods.

Domergue (1973) reported frogs in the diet of *Liopholidophis lateralis*, and that is confirmed by all my observations. Three *lateralis* in the RNP sample contained food: MCZ 180344 (SVL 547 mm) contained one *Mantidactylus betsileanus* (Ranidae; a terrestrial, diurnal frog) swallowed tail first; MCZ 180345 (SVL 517 mm) contained one *Boophis madagascariensis* (Rhacophoridae; at least sometimes terrestrial when inactive diurnally) swallowed head first; MCZ 180350 (SVL 543 mm) contained remains of one *Ptychadena mascareniensis* (Ranidae; terrestrial/semiaquatic, diurnal) swallowed head first. AMNH 60675 (SVL 537 mm) contained one *Ptychadena mascareniensis* swallowed head first and one other small unidentified frog swallowed tail first. In contrast to other species of terrestrial *Liopholidophis* with recorded food items, *lateralis* seems to consume terrestrial microhylids infrequently (the semiaquatic *L. sexlineatus* is another exception). This probably reflects the more open habitats frequented by *lateralis* and the absence of microhylids in those habitats. The frogs recorded in the diet are frequently encountered in open or secondary habitats, as is *L. lateralis*.

Domergue (1973) reported clutch sizes of 6–13 in *Liopholidophis lateralis* and observed several clutches at the end of November/beginning of December (locality not given). Hence, the species is oviparous. Two specimens from the RNP, MCZ 180348 (SVL 583 mm) and 180344 (SVL 547 mm) collected 6–11 January, contained nine and seven enlarged ovarian eggs, respectively. MCZ 180375 (SVL 491 mm), collected 13 January near Midongy Atsimo (Appendix), contained seven enlarged ovarian eggs.

*Remarks.* Most specimens of *lateralis* have two apical pits on all scale rows between the dorsolateral light stripes. Occasional specimens appeared to have no apical pits (e.g., MCZ 180380), and in still

others the number of pits and their consistency varied. When present, the pits continue onto the dorsal caudal scales to the tail tip.

*Liopholidophis infrasignatus*  
(Günther)

Figures 23, 27–29

*Ptyas infrasignatus* Günther, 1882: 263 (Type locality, "Arkafana, Eastern Betsileo" [corrected to "Ankafana, Betsileo" by Boulenger, 1893:247; see "Remarks" and Cowan, 1883:147]). Lectotype by present designation, BMNH 1946.1.7.57, collected by Reverend W. D. Cowan.

*Dromicus baroni* Boulenger, 1888:104 (Type locality, "Madagascar"). Holotype, BMNH 1946.1.7.67 (old number 87.12.22.38), collected by R. Baron. [examined] **New synonymy.**

*Tropidonotus stumpffii* (Boettger), part: Günther, 1890:70; Boulenger, 1893:247–248 (*Ptyas infrasignatus* Günther listed as a synonym; specimens b–d [=BMNH 1946.1.7.56–58, types of *infrasignatus*] and k–m [=BMNH 95-10.29.53–55]).

*Liopholidophis lateralis* (Duméril, Bibron, and Duméril), part: Mocquard, 1909:95 (*Ptyas infrasignatus* Günther listed as synonym). Guibé, 1958:243 (*Ptyas infrasignata* [sic] Günther listed as a synonym).

*Liopholidophis stumpffii* (Boettger), part: Parker, 1925: 391 (*L. infrasignatus* (Günther) listed as a synonym in footnote).

*Liopholidophis thieli* Domergue, 1973:1405 (Type locality, "fish ponds of the Perinet Tropical Forestry Station, 900 m elevation). Holotype, MNHN 1973-332. **New synonymy.** Brygoo, 1983:55, 1987: 24; Nicoll and Langrand, 1989:117, 130; UICN/PNUE/WWF, 1990:223; Glaw and Vences, 1992: 266, 1994:338.

*Notes on Types and Designation of Lectotype.* *Ptyas infrasignatus* Günther is here considered the valid name for the species referred in recent literature to *Liopholidophis thieli* Domergue (references cited in synonymy). The type locality of *infrasignatus* is about 25 km ENE of the RNP, whereas the type of *thieli* is from Perinet (=Andasibe). Based on comparison of the types of *infrasignatus* and *thieli*, I conclude that they and the series from the RNP assigned to *infrasignatus* represent the same taxon. Additional comments on the type of *thieli* are given later (see "Notes on Type Specimens of Junior Synonyms").

The syntypes of *Ptyas infrasignatus* are BMNH 1946.1.7.56–58, two adult females and adult male, respectively [old numbers



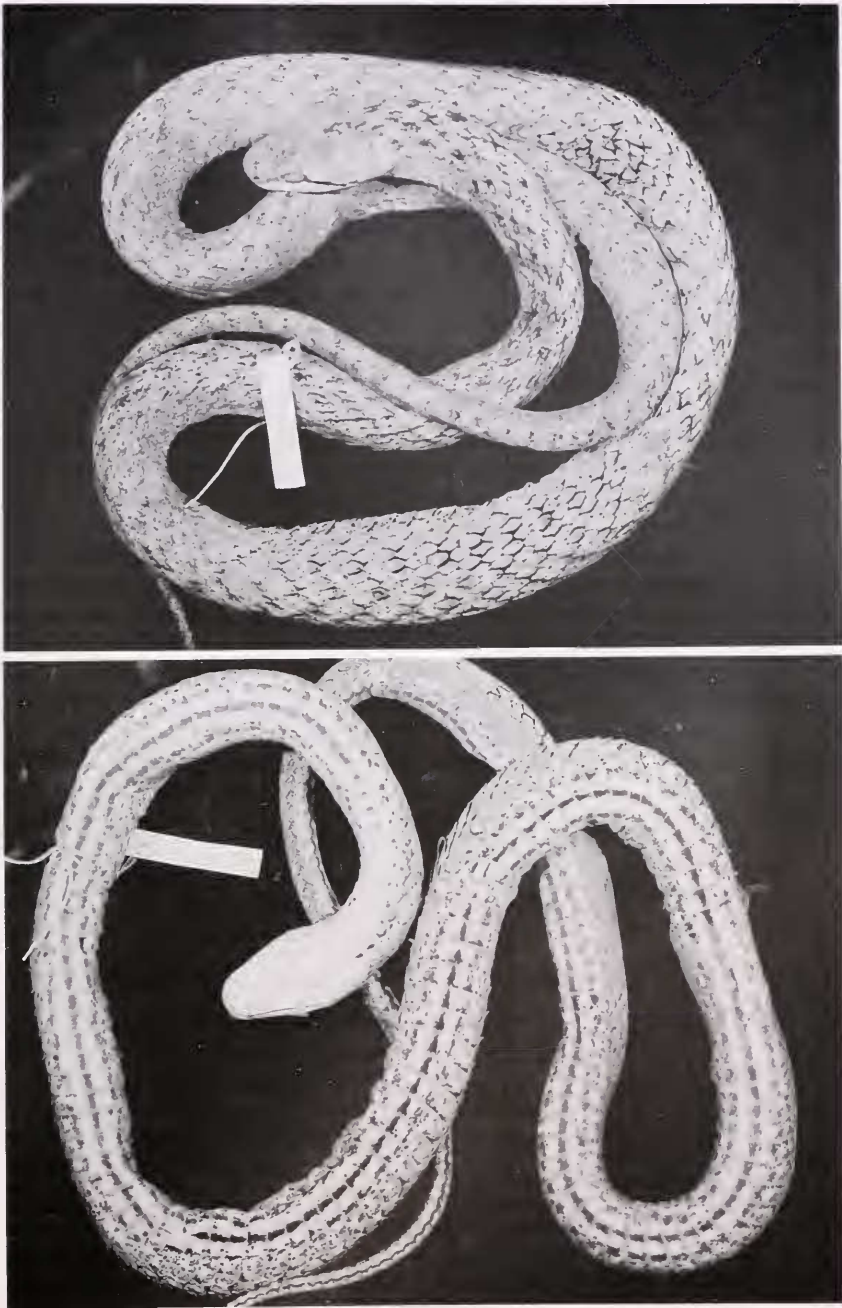


Figure 27. *Liopholidophis infrasignatus* (Günther), lectotype (BMNH 1946.1.7.57) from "Ankafana, eastern Betsileo." Dorsal and ventral views.

82.2.25.59-64)), collected by Rev. W. D. Cowan. The largest of the two females, BMNH 1946.1.7.57, is here designated the lectotype (Figs. 27-28). Characteristics of these specimens are reported here in order of the series, 1946.1.7.56-58. These are the largest specimens of *infrassignatus* reported (Domergue, 1973, as "thieli") or studied herein, with measurements (mm) and proportions as follows (total length, tail length, tail length as a percentage of total): two females (904, 215, 24%; 920, 208, 23%), male (727+, 121+). Ventrals 155, 156, 152.5, in each case preceded by two pre-entrals. Subcaudals 71, 67, 46+. Dorsal scales in 19-19-17 rows. One preocular, two postoculars, and 2-2 temporals. Eight supralabials (4-5 touching eye); 10-10 (females) or 9-10 (male) infralabials. Divided anal. Maxillary teeth 21, 23, 23, followed by two enlarged, ungrooved fangs.

General dorsal color light brownish with occasional scattered darker flecks (nowhere dense). Indistinct light dorsolateral lines (most evident under fluid) on neck and anterior 20% of body. Thin dark postocular bar from posteroventral corner of eye, across penultimate supralabial, and ending on anteroventral corner of ultimate supralabial. Otherwise, supralabials light, immaculate (dorsal ground color encroaches onto ultimate one). Infralabials and gulars immaculate yellowish white. Venter yellowish white with dense series of dark spots and markings, increasing posteriorly (similar to variation within the RNP sample), tending to form midventral series or line in females; dark encroachment of dorsal color onto lateral edge of ventrals, and an indistinct series of spots laterally on ventrals (except male).

*Diagnosis.* *Liopholidophis infrassignatus* differs from members of the *sexlineatus* group in having 19-19-17 dorsal scale rows (vs. 17-17-15). It has a relatively short tail and low numbers of subcaudals compared to other members of the *stumpffi* group (Table 2). The dorsolateral light stripes are anteriorly on rows 5-6, by which *infrassignatus* differs from *lateralis* (rows 3-5) and *stumpffi* (rows 4-5). *Ep-*

*istibes* differs from *infrassignatus* in having a relatively long tail and higher ventral and subcaudal counts (Table 2 and *epistibes* account).

*Distribution.* Scattered localities on the eastern escarpment and eastern edge of the high plateau, as shown on maps (for *Liopholidophis* "thieli") presented by Domergue (1973:1398) and Glaw and Vences (1994:336). From at least the vicinity of Midongy Atsimo (23°35'S, 47°01'E) in the south (Appendix) to Antongil Bay (Nosy Mangabe) in the north (Domergue, 1973:1409). Most localities appear to be upland sites, 600-1,200 m elevation. The Nosy Mangabe locality is <100 m (Domergue, 1973:1409), whereas the type locality for *infrassignatus* is possibly as high as 1,600 m (see "Remarks"). *Liopholidophis infrassignatus* appears to be widespread within the RNP, and turns up at most forested localities with sufficient sampling (known elevational range within the park approximately 800-1,150 m).

*Description.* The following description is based on examination of 19 females and 11 males, including syntypes of *Ptyas infrassignatus* Günther and the holotypes of *Dromicus baroni* Boulenger and *Liopholidophis thieli* Domergue; ranges of variation for size, tail proportions, and ventral and subcaudal counts incorporate data for *L. thieli* given by Domergue (1973:table II). Measurements, proportions, and scutellation are summarized in Table 2. Largest specimen the female lectotype (BMNH 1946.1.7.57), 920 mm total length, 208 mm tail length (23% of total); largest male (BMNH 1946.17.58, a paralectotype), 727+ mm total length, incomplete tail 121+ mm. Proportional tail length not strongly sexually dimorphic, 23-27% of total length in males, 21-24% in females. Dorsal scales smooth, in 19-19-17 rows; 0-2 apical pits on different scales within an individual. Scale row reduction from 19 to 17 rows by fusion of rows 3 + 4 (occasionally loss of row 4, and one instance of 4 + 5 fusion) at the level of ventrals 78-94 (N = 18). Ventrals 146-156 in males, 144-161 in females. Anal plate

divided. Subcaudals 66–81 in males, 62–73 in females. Eight (rarely seven) upper labials with 4–5 touching eye. Lower labials usually 10–10 (N = 22), with other variants being 8–8 (1), 9–9 (1), 9–10 (4), and 10–11 (2), the first pair in contact behind the mental, 1–5 (occasionally 1–4) touching an anterior genial, 5–6 (occasionally 4–5) touching a posterior genial. Anterior genials shorter than posterior genials. Loreal present. Preocular single. Temporals 2 + 2 (rarely 1 or 3 anterior or posterior temporals).

Body slightly higher than wide; ventrolateral edge of body angulate. Head slightly wider than neck. Pupil round. Eye moderately large, its diameter slightly greater than the distance from eye to posterior edge of nostril ( $\bar{x} = 1.21 \pm 0.1$ ; range = 1.06–1.44; N = 19).

Scattered pits present on head scales, most consistently and densely on circumorbital scales and on prefrontals and nasals; in some specimens, they are liberally sprinkled over most of the head plates and supralabials except for the central parts of the parietals and frontal.

**Dentition.** Maxillary teeth 20–25 + 2 (N = 28;  $\bar{x} = 22.3 \pm 1.38$  prefang teeth). Diastema absent; gap < 1 tooth width separating tooth row from enlarged fangs. Ungrooved fangs not offset from tooth row, twice as large as the posteriormost maxillary teeth; having a rounded anterior surface (except for distal portion, which has a cutting edge) and a flattened knifelike posterior surface. The tips of the fangs are slightly compressed. The skulls of two females, MCZ 180357 and 180370, have, respectively, 14–14 and 15–16 palatine teeth, 30–28 and 30–30 pterygoid teeth, and 27–26 and 28–28 dentary teeth.

**Hemipenis (Fig. 36).** Deeply bilobed, noncapitate, acalyculate (entirely spinose), with a deeply bifurcate centrolineal sulcus spermaticus. Distal tips of the lobes with a central “umbelliform” depression.

**Coloration in Life (see Glaw and Vences, 1994:pl. 349 [L. “thieli”], which is similar to many specimens from the RNP).** MCZ 180355 (female): Dorsum



Figure 28. *Liopholidophis infrasignatus* (Günther). Lateral view of head of lectotype (BMNH 1946.1.7.57).

olive brown, with indistinct indication of golden dorsolateral stripes anteriorly. Black postocular bar to corner of mouth, crossing middle of last two supralabials (see Domergue, 1973:fig. 6). Venter dull grayish yellow (tending to grayish white), with thin black longitudinal markings tending to form lines midventrally and ventrolaterally. Black speckling on outer edges of ventrals. A few dorsolateral black specks forming roughly two longitudinal rows just behind head (ca. 5–10 cm). Upper labials whitish, suffused with brown anteriorly. Lower labials whitish.

MCZ 180354 (male): Similar to MCZ 180355, but with orange wash on venter, especially posteriorly. Ventral dark marking forms midventral dark line on most of body and tail.

The dorsal ground color in the RNP sample ranges from dull grayish to olive brown to rich golden brown. Some dorsal scales, especially medially on the anterior body, have white scale borders similar to those in *stumpffi*, *epistibes*, and *lateralis*; these do not appear as constant or as vivid in *infrasignatus* as in these other species. The postocular bar usually crosses the last two supralabials but sometimes ends on the penultimate one; often there is a separated extension on the ultimate supralabial (Figs. 23, 28) The dorsolateral light stripes may be evident primarily on the anterior part of the body, most of the body, or they may be rather indistinct. Most specimens have some indication of black spots dorsolaterally on the anterior trunk (usually occu-

pying one dorsal scale or less); these usually fade by midbody but occasionally are present the length of the body. A ventral orangish wash is characteristic of many specimens.

*Coloration in Preservative.* Grayish brown to grayish olive dorsal ground color, usually with some indication of dorsolateral light stripes anteriorly. Dorsolateral stripes anteriorly on rows 5–6, not confluent with light color of throat (Fig. 23), usually fading by midbody. A blackish postocular stripe from the eye to the corner of the mouth is universally present, and dark punctations are sometimes present on the dorsum, especially anteriorly. Supralabials whitish except dorsally, where the dorsal ground color encroaches; infralabials and throat region whitish. Venter dull white with dark grayish black peppering, spotting, or streaking, usually forming a continuous dark midventral line (Figs. 27, 29; see also Domergue, 1973:fig. 7). Dark grayish pigment usually encroaches upon the venter from the flanks, occasionally reaching the midventer, and sometimes forming a broken dark line on the lateral edges of the venter; in some specimens, most of the venter is dark gray, but the midventral line is usually still evident in such specimens. Smaller specimens tend to have light venters, suggesting an ontogenetic component to development of the ventral pigmentation. The stratum corneum is easily lost in preservative, giving a grayish cast to the dorsum.

*Natural History.* *Liopholidophis infrasignatus* is diurnal and terrestrial. This was the most frequently encountered diurnal snake in forested areas of the RNP, usually active or sunning on trails from early morning to later afternoon; it was found in primary montane rainforest, 900–1,050 m, and in one higher elevation (1,130 m) short-stature forest, but not in secondary forests or open habitats. Other species, such as *L. sexlineatus* and *L. lateralis*, are possibly numerically more abundant in open habitats such as rice fields, marshes, and secondary forests.

*Liopholidophis infrasignatus* bites in defense and also dorsoventrally flattens the anterior portion of the body. Domergue (1973:1409) reported neck flattening, as well as inflation of the body to reveal white borders of the dorsal scales.

Four *Liopholidophis infrasignatus* contained one food item each, all swallowed head first: MCZ 180370 (SVL 552 mm) contained the hind limbs of a large *Plethodontohyla inguinalis*, a large terrestrial microhylid frog; MCZ 180373 (SVL 216 mm) and MCZ 180374 (SVL 330) each contained remains of *Plethodontohyla aluaudi*, a small terrestrial microhylid; MCZ 180359–60 (food regurgitated into a common collecting bag) (SVLs 461 and 432 mm, respectively) contained a *Chamaeleo nasutus*. Domergue (1973) reported frogs in the diet of *Liopholidophis "thieli"* (= *infrasignatus*).

Four females in the RNP sample were gravid: MCZ 180370 (SVL 552 mm), collected 21 December contained small yolking follicles; MCZ 180372 (SVL 530 mm), collected 20–23 November, and MCZ 180356 (SVL 555 mm), collected 10 December, contained six and three, respectively, large, but nonoviductal yolking follicles; MCZ 180362 (SVL 609 mm), collected 19 December, contained nine shelled eggs, one of which contained an embryo in Zehr (1962) stage 18. Glaw and Vences (1994) reported that gravid females of *L. infrasignatus* (as *L. thieli*; locality not stated) collected in November laid six to seven eggs. Domergue (1973) reported six eggs in a female (SVL 546 mm) collected in November, a clutch of six laid by a female (SVL 593 mm) at the end of March, and a clutch of seven laid by a female (SVL 567 mm) in mid-November; all specimens were from Perinet, but details on captive maintenance were not given.

*Remarks.* The type locality of *Ptyas infrasignatus*, Ankafana (=Ankafina), is a regional name for a forest just west of Tsarafidy (Carleton and Schmidt, 1990) near the eastern edge of the high plateau. It lies at approximately 1,600 m elevation ac-

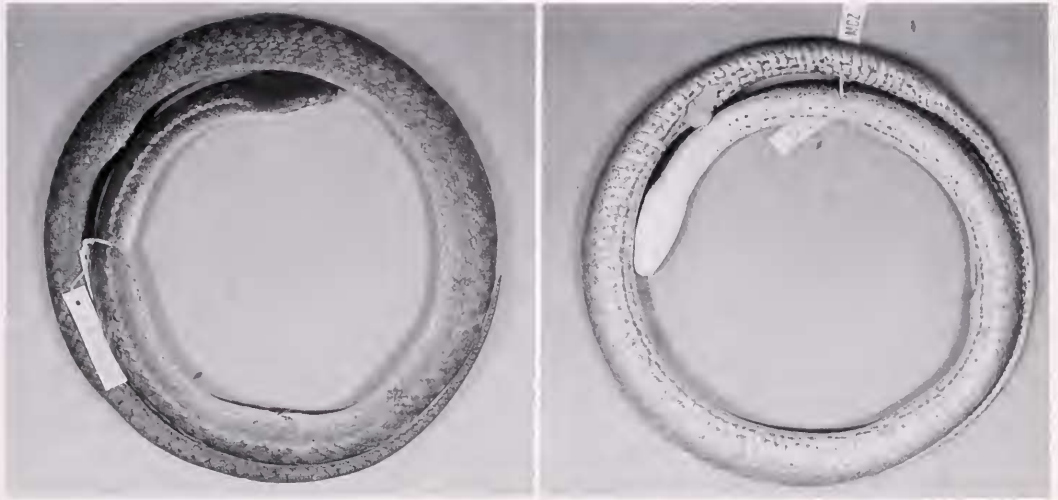


Figure 29. *Liopholidophis infrasignatus* (Günther). Dorsal and ventral views of specimen from the RNP (MCZ 180359).

according to MacPhee (1987).<sup>12</sup> Other recent specimens of *Liopholidophis infrasignatus* have come from the same vicinity (Domergue, 1973:1405; two specimens of "thieli" in table II from Tsarafidy). Raxworthy and Nussbaum (1994:8) cited MacPhee (1987:5) as the authority that the correct name for this locality is "Ankafina," not "Ankafana," based on the designation in descriptions of small mammals collected by Cowan at this locality. However Carleton and Schmidt (1990) used the two names interchangeably. Boulenger (1893:247) corrected Günther's (1882) erroneous designation "Arkafina" to "Ankafana." Cowan (1883) himself was probably responsible for the confusion: in the text he refers at least twice to the locality as "Ankafana" (e.g., p. 147), but on the accompanying map it is plotted as "Ankafina."

<sup>12</sup> The elevation is 1,300–1,540 m according to Raxworthy and Nussbaum (1994). The FTM 1:1,000,000 map shows a peak at this locality of 1,679 m. On Cowan's (1883) map, Tsarafidy is denoted as "Itsafidy."

Domergue (1973) reported occasional presence of two apical pits in *Liopholidophis "thieli"*. I noted the presence of 0–2 apical pits, the number highly variable within and between individuals. Parker (1925:391, footnote) observed much variation in apical pit occurrence in species of the *stumpffi* group; he noted that one of the three syntypes of *infrasignatus* had apical pits (number not stated), whereas the other two lacked them.

Domergue (1973) reported that the Malagasy name *Menamaso* ("orange eye") was used for *Liopholidophis "thieli"* in the Perinet region, in reference to the often-orangish coloration of the iris. The name *Mandodrano* is used in the RNP area.

*Notes on Type Specimens of Junior Synonyms.* Because I resurrect the name *Ptyas infrasignatus* from synonymy and place two names as new synonyms of it, I here provide notes on the relevant type specimens of junior synonyms. References are given in the synonymy.

1. *Dromicus baroni* Boulenger (holotype, BMNH 1946.1.7.67 [old number 87.12.22.38], adult female): Total length 734 mm; tail length 167 mm; tail as a per-

centage of total length, 23%. Ventrals 158 (+2 preentrals), subcaudals 69, one preocular, two postoculars, 2-2 temporals. Supralabials 8-8 (4-5 touching eye), right infralabials 10 (left side damaged). Dorsal scales ?-19-17. Maxillary teeth 24 + 2. Dorsum dark grayish or greenish black, somewhat lighter anteriorly; tail not differentiated in color. Vague indication of some darker spots or markings when specimen under fluid, but this is subtle; anteriorly, there are dark spots on the neck, forming indistinct reticulated pattern, but no light dorsolateral stripes are evident. Each dorsal scale very finely speckled with light yellowish spots, giving overall velvety appearance ("powdered with yellowish"; Boulenger, 1888:104). Black postocular bar extending diagonally down across last supralabial. Otherwise, supralabials white (some grayish suffusion on anterior one or two). Infralabials and gular region white. Dorsal pigment encroaches onto outer 20-25% of each ventral edge; medial to this and not cleanly separated is a series of large irregular dark splotches (one pair per ventral); midventrally, a series of oblong dark spots forms a more or less continuous midventral line (see Boulenger, 1888:pl. V, fig. 5). Posteriorly on venter, dark pigment increases; underside of tail mostly dark (concentrated midventrally, lighter laterally).

The type of *Dromicus baroni* has an unusual coloration and pattern from other *Liopholidophis*, and its placement in the synonymy of *Ptyas infrasignatus* is provisional. Based on coloration, the specimen could be considered a rather unusual variant of either *infrassignatus* or of *stumpffi sensu lato*, where *baroni* has previously been placed (e.g., Boulenger, 1898) (*epistibes* in this work). (Interestingly, the holotype of *L. thieli* [= *infrassignatus*] shows fine stippling of yellowish similar to, but less distinct than, that of *baroni*.) However, unlike all other specimens of either *infrassignatus* or *epistibes* studied, the type of *baroni* has no indication of light dorsolateral stripes, and none was mentioned in the original description (Boulenger,

1888). The proportional tail length (23% of total) and subcaudal counts (69) of *baroni* are within the range of other *infrassignatus* females and considerably outside the range of *epistibes* females (see Table 2). The position of the postocular dark stripe extending diagonally downward across the last supralabial, rather than across its upper border, is also typical of *infrassignatus* rather than *epistibes* (cf. Figs. 8, 23, 28). Hence, the name *baroni* is synonymized with *infrassignatus*. Its status should be re-evaluated if additional specimens with precise locality data and having the unusual coloration of *baroni* are discovered.

2. *Liopholidophis thieli* Domergue (holotype, MNHN 1971-332, adult male with everted hemipenes): Total length 695 mm; tail length 169 mm; tail as a percentage of total length, 24%. Ventrals 144 (+2 preentrals), subcaudals 69, anal divided; one preocular, two postoculars, 2-2 temporals. Supralabials 8-8 (4-5 touching eye), infralabials 10-10. Dorsal scales 19-19-17; dorsal reduction by fusion of rows 3 + 4 at ventrals 75-72. Maxillary teeth 24 + 2; no diastema. All of these values are typical of *infrassignatus* (Table 2).

The coloration of the type of *thieli* is identical to that already described for *infrassignatus*, although it appears somewhat darkened, perhaps as a preservation artifact. The venter of MNHN 1971-332 is strongly patterned, with a median and a lateral series of irregular half-moon-shaped blotches, as well as other irregular spotting. This pattern is within the range of variation observed in the RNP sample of *infrassignatus*.

Although Domergue (1973) properly resurrected *Liopholidophis stumpffi* (Boettger) from the synonymy of *L. lateralis*, failure to examine type material of previously described nominal taxa caused confusion of two species under the name *stumpffi*, discussed earlier, as well as resulting in the description of *thieli* for a previously described taxon. Direct comparison of the types reveals that *Liopholidophis thieli* Domergue, 1973, is identical with *Ptyas infrassignatus* Günther, 1882,

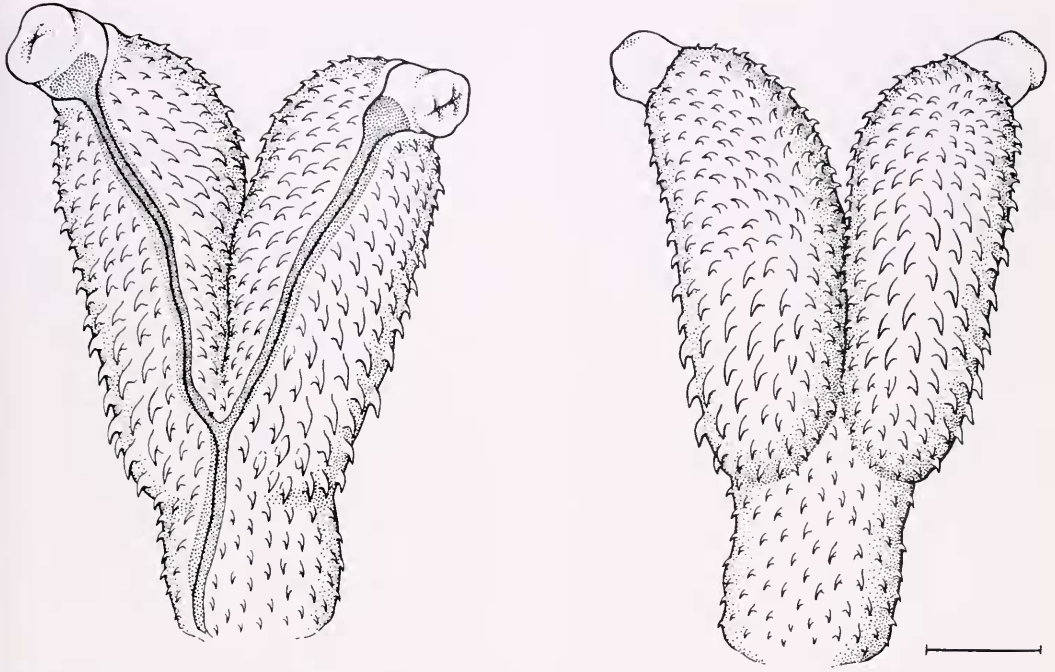


Figure 30. Hemipenis of *Liopholidophis rhadinaea*, new species. Fully everted organ of MCZ 180394 (from Talatakeley in the RNP), shown in sulcate (left) and asulcate (right) views. Scale bar = 1 mm.

a species variously subsumed under *lateralis* or *stumpffi* for more than a century (Günther, 1890; Boulenger, 1893; Mocquard, 1909; Parker, 1925; Guibé, 1954, 1958). Hence, *thieli* Domergue is a junior synonym of *infrasignatus* Günther.

#### HEMIPENIAL MORPHOLOGY IN LIOPHOLIDOPHIS

Everted hemipenes of all currently recognized nominal species of *Liopholidophis* are described here. Brief comparisons to the corresponding inverted organs are given for some taxa as necessary.

##### The *sexlineatus* Group

*Liopholidophis rhadinaea* (Fully Everted Left Organ of MCZ 180394; Fig. 30). The organ is deeply bilobed, non-capitate, acalyculate (entirely spinose), with small cylindrical awns at the tips of

the lobes (described later) and a deeply bifurcate centrolineal sulcus spermaticus. Total length of the everted organ approximately 6.5 mm, bilobed for the distal 2.5 mm. Sulcus spermaticus forked distally for 3 mm. No basal pockets or lobes.

The sulcus spermaticus is a deep groove, bifurcate for about  $\frac{1}{2}$  its length, with the branches terminating on the same side of the organ at the base of the apical awns (centrolineal in orientation). The tip of each branch broadens slightly, resulting in funnel-shaped distal end of each branch.

The stalk of the organ below the lobes is covered on all sides with small hooked spines. The stalk abruptly broadens slightly just below the sulcus division, the spines also coincidentally increasing in size (spines here about twice as large as those on the base of the stalk). The lobes, including the crotch and inner and outer surfaces, are covered with hooked spines up to the distal tips of the branches of the sulcus. The spines

are arrayed more or less in longitudinal rows.

Distally, beyond the tips of the branches of the sulcus spermaticus, each lobe has a nude, cylindrical projection (*cylindrical awn*), each somewhat <1 mm in length (i.e., considering only the nude portion); the distal tip of each awn is more or less flat but is slightly dimpled. These awns are not set off from the tips of the lobes except in lacking ornamentation (nude) and in projecting beyond the ends of the sulcus tips.

Dowling (1959) and Dowling and Savage (1960) used the term *awn* for elongate, pointed projections from the apex of colubrid hemipenes. My use of the term *cylindrical awn* for the structures in *Liopholidophis rhadinaea* suggests a different shape but does not necessarily imply homology with those as seen, for example, in *Tropidoclonion* (Dowling, 1959). *Liopholidophis doliocercus* (see later) has tapered apical structures similar to, but less differentiated than, those of *L. rhadinaea*. The form of the apical structures in *rhadinaea* are unique among known colubrid hemipenes.

Although the awns on the hemipenes of *rhadinaea* might be construed as an artifact of overeversion, two other specimens with well-everted organs (MCZ 180392, 180396) had similar ornamentation, whereas a specimen with clearly uneverted tips to the lobes (MCZ 180402) does not show these structures. To more fully characterize these peculiar structures, the ventral lobe of an inverted hemipenis (MCZ 180389) was slit midventrally and examined *in situ*. The hemipenis extends to the level of the suture between subcaudals 6–7. The awn appears as a nude region (slightly >1 subcaudal scale in length) beyond the spinous portion of the lobe. The sulcus, in the dorsolateral wall of the lobe, ends in a slight expansion at the proximal end of the nude region.

*Liopholidophis doliocercus* (Fully Everted Right Organ of MCZ 180405; Fig. 31). The organ is deeply bilobed, non-

capitate, and acalyculate (entirely spinose). Sulcus spermaticus deeply bifurcate, centrolineal. Total length of the everted organ 19 mm, bilobed for the distal 10.5 mm. Sulcus spermaticus forked distally for approximately 9.5–10 mm. No basal pockets or lobes.

The sulcus spermaticus is a deep groove, forked for about half of its length, the branches passing distally on the same side of the organ (centrolineal). Distal tips of the forks not expanded, ending at edge of an apical nude area.

Stalk of organ below the lobes on sulcate surface ornamented with tiny hooked spines; these are arrayed in a few rows paralleling the basal undivided part of the sulcus, and with spines generally covering the stalk to one side of the sulcus. "Lateral" surface of stalk between sulcate and asulcate surfaces largely nude (a few scattered small spines).

The asulcate surface of stalk has a median patch of spines from near the base of the organ nearly to the point at which the organ divides. A highly unusual feature of this patch is that each spine appears to be recessed within a small pocket.

Distal to division of the organ, the facing surfaces of the lobes are closely appressed and nude (as seen by prying the lobes apart), but distally the facing surfaces diverge and are ornamented with spines on all sides.

At the level of the division of the sulcus spermaticus, the body of the organ is abruptly expanded (from a width of approximately 4.5 mm to approximately 8.5 mm). Concomitantly, the size of the spines abruptly increases, although toward the tips of the lobes spines again gradually become smaller. The narrow, distal portion of each lobe (especially on asulcate side and "crotch" side) is only sparsely covered with tiny spines. Tips of the lobes nude and with a median dimple.

The narrow distal portions of the hemipenial lobes in *Liopholidophis doliocercus* appear similar to the apical awns of *L. rhadinaea*, with two exceptions (cf. Figs.



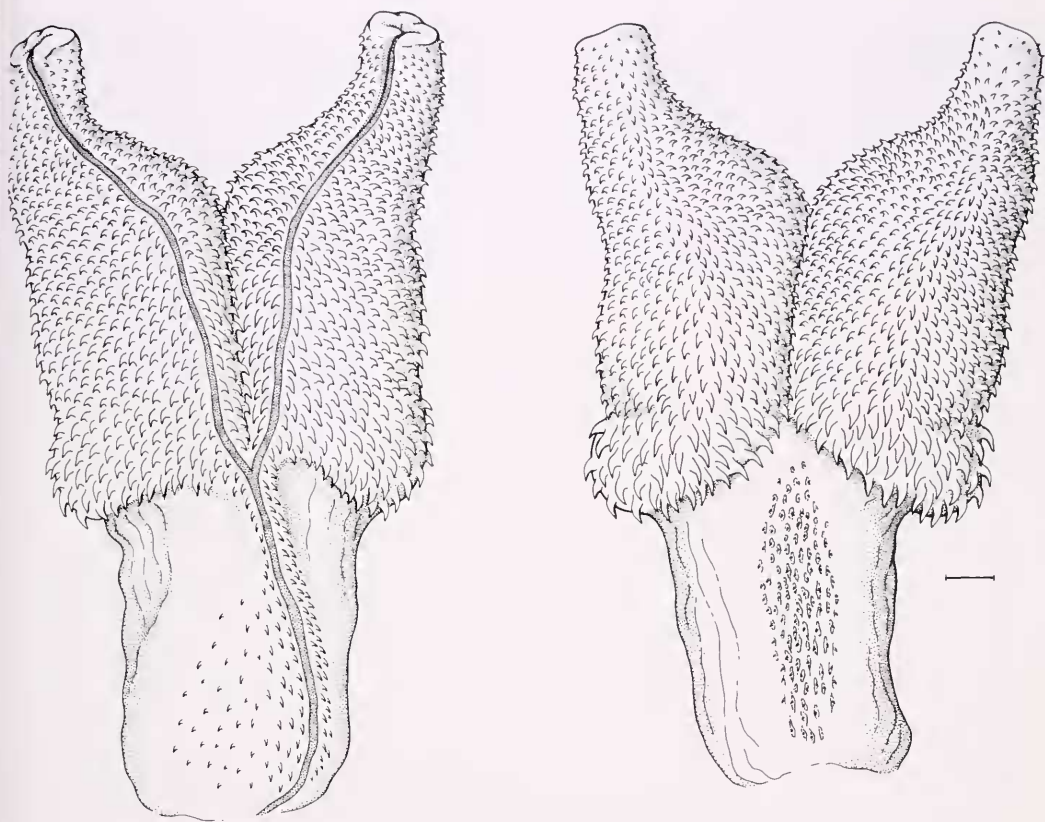


Figure 31. Hemipenis of *Liopholidophis doliocercus* (Peracca). Fully everted organ of MCZ 180405 (from Talatakey in the RNP), shown in sulcate (left) and asulcate (right) views. Scale bar = 1 mm.

30–31): (1) in *dolioscercus* the narrow portion has a sparse covering of tiny spines (nude in *rhadinæa*) and (2) the unexpanded tips of the sulcus spermaticus extend to the edge of the distal nude area in *dolioscercus*, whereas in *rhadinæa* the tips of the sulcus are expanded and end at the base of the apical awns.

*Liopholidophis grandidieri* (Fully Everted Right Organ of MCZ 180297; Fig. 32). The organ was nearly completely everted upon preservation but subsequently everted fully using the technique of Pesantes (1994).

The organ is deeply bilobed, noncapitate, acalyculate (entirely spinose), and with a deeply bifurcate centrolineal sulcus

spermaticus. The organ is 11 mm total length, bilobed for the distal 5 mm. The sulcus spermaticus is bifurcate for the distal 6 mm. No basal pockets or lobes are present.

The sulcus spermaticus is a broad, deep groove, forked for about  $\frac{1}{2}$  of its length, with the branches passing distally on the same side of the organ (centrolineal). Distal tips of the forks not expanded, ending at the distal tips of the lobes.

Entire organ ornamented with hooked spines, smallest on the lobes, with an array of larger spines encircling the organ at the point where the lobes join (approximately 8–10 enlarged spines around base of each lobe from sulcus to middle of asulcate side).

Spines sparser on extreme distal tips of the lobes than the adjacent proximal portions. Spines sparser in a band around the middle of the organ (immediately proximal to the lobes) than on the base of the stalk or on the lobes. A small nude area is present on each "lateral" surface of stalk just proximal to the union of the lobes. Base of stalk with small dense arrays of spines on all sides, somewhat larger and less dense on asulcate than on sulcate side.

The stalk of the organ is of uniform width (i.e., no abrupt expansion, as seen in *dolicocercus* and *rhadinaea*). After division of the organ, the lobes diverge gradually and are densely ornamented with spines on all sides.

***Liopholidophis sexlineatus*** (*Fully Everted Right Organ of MCZ 180337; Fig. 33*). The organ is deeply bilobed, noncapitate, acalyculate (entirely spinose), with a deeply bifurcate centrolineal sulcus spermaticus. Total length of the everted organ approximately 10 mm, bilobed for the distal 4 mm. Sulcus spermaticus forked distally for 4.5 mm. No basal pockets or lobes.

The sulcus spermaticus is a deep groove, bordered by thickened, overhanging lips; bifurcate for about  $\frac{1}{2}$  its length, with the branches terminating abruptly about 1.5 mm short of the tips of the lobes on the same side of the organ (hence, centrolineal). Basal undivided portion of sulcus spermaticus bordered on either side by dense array of small hooked spines. Subsequent to division of the sulcus, these spines become gradually larger to approximately the midpoint of the lobes, then decrease in size toward the tips of the lobes.

The basal  $\frac{1}{2}$ - $\frac{2}{3}$  of the stalk on the asulcate side bears a patch of small hooked spines; distal half of the stalk on the asulcate side is sparsely ornamented with spines, with large more or less nude areas. "Lateral" surface of stalk between the asulcate spinous portion and the sulcus is mostly nude (a few scattered spines, mostly concentrated proximally). Proximal portion of the asulcate and "lateral" surfaces

of each lobe with approximately 12 somewhat enlarged hooked spines; more distal portion of lobes entirely spinose with smaller spines. The facing surfaces of the lobes are entirely spinose, but the crotch has a small nude area between the lobes; on the asulcate side, the nude area in the crotch separates the enlarged spines encircling the base of each lobe from the corresponding spines of the other lobe.

Beyond the distal tips of the branches of the sulcus spermaticus the lobes have a somewhat unusual ornamentation, which is restricted to the apex of the sulcate side (i.e., not encompassing the apex on the asulcate side, which is simply spinose as just described). The apexes bear 8-10 enlarged papillae or folds, each capped by a single spine that is approximately the same size as spines on the adjacent, nonpapillate portions of the lobes. Between the papillae, the organ appears nude. The overall effect of this ornamentation under low magnification is to give the apexes of the asulcate surface a somewhat rugose appearance.

The papillae on the hemipenis of *Liopholidophis sexlineatus* are not similar to the "apical papillae" described by Dowling (1959), which are merely pointed, awnlike structures at the tips of some colubrid hemipenes (one per lobe). However, they are somewhat similar to the spinulate papillae on the lobes of *Psomophis* hemipenes (Myers and Cadle, 1994:13). Unlike *Psomophis*, in which enlarged papillae are capped by minute spinules, the papillae of *L. sexlineatus* are capped by a spine approximately the same size as other distal spines on the organ. Based on the minuteness of the spinules and seemingly weak mineralization of some papillae when micromanipulated, Myers and Cadle (1994:13) hypothesized that the spinulate papillae on *Psomophis* hemipenes were derived from fully mineralized spines. Such a derivation seems less likely for the spinose papillae of *L. sexlineatus*, in which the spines on the papillae are not noticeably smaller than other distal spines. The diversity of apical structures in the *sexli-*

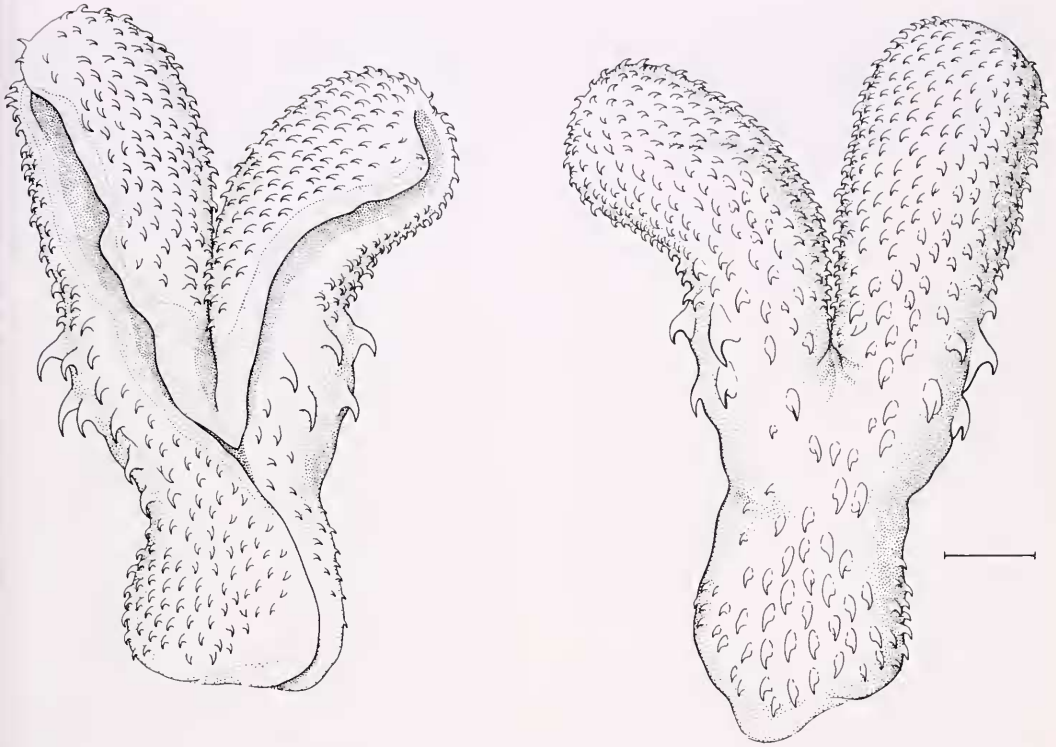


Figure 32. Hemipenis of *Liopholidophis grandidieri* Mocquard. Fully everted organ of MCZ 180297 (from Mt. Maharira in the RNP), shown in sulcate (left) and asulcate (right) views. Scale bar = 1 mm.

*neatus* group (cf. *rhadinaea* and *dolicocercus*) makes the homology and origin of these structures difficult to discern with present knowledge.

***Liopholidophis pinguis*** (*Everted Right Organ of MCZ 11701, Prepared from the Inverted Organ by the Method of Pesantes [1994]*). Before the organ was removed, it extended to approximately the middle of subcaudal 9 and bifurcated at the level of the suture between subcaudals 5 and 6. The major retractor muscle divides at about the base of subcaudal 11. The ventral lobe of the left hemipenis was examined *in situ* by making a midventral incision.

The organ is deeply bilobed, noncapitate, acalyculate (entirely spinose), with a deeply bifurcate centrolateral sulcus sper-

maticus. Total length of the everted and injected organ approximately 15 mm, bilobed for the distal 6.5 mm. Sulcus spermaticus forked distally for 10 mm. No basal pockets or lobes. Stalk and lobes narrow, with no abrupt expansions. No especially enlarged spines anywhere on organ.

The sulcus spermaticus is a broad, deep groove, bordered by thickened, overhanging lips; bifurcate for about  $\frac{2}{3}$  its length, with the branches terminating at the tips of the hemipenial lobes on the same side of the organ (centrolateral). There seems to be slight displacement of the branches toward the outer sides of the lobes, but this may be an artifact of the preparation method; the sulcus in the opened lobe of the inverted organ was on the lateral side of the lobe, as typical for centrolateral sulci.

Basal undivided portion of sulcus bordered on either side by dense array of short, thick, curved spines. Similar spines line the outer border of the sulcus from the base to the tip, and the mesial border of the forks of the sulcus beginning at the fork; the latter are continuous with the spinous portion of the lobes, and afford the only continuity between the spinous portions of the lobes. Spines are short spikes sitting atop a broad base. Subsequent to division of the sulcus, the spines become gradually larger to approximately the midpoint of the lobes, then decrease in size toward the tips of the lobes. There are no abruptly enlarged spines. The inner side of the crotch of the organ nude for approximately 25% the length of the lobes, as is the mesial portion of the stalk of the organ between the division of the sulcus and the crotch of the organ. Spinous portions of lobes mesially entirely separated by nude area in crotch.

Asulcate side of stalk with sparse covering of short hooked spines; crotch of organ on asulcate side nude. Body of lobes on the asulcate side with dense array of spines, longest proximally, gradually decreasing in size distally; a short, nearly nude section at base of each lobe has only a few scattered spines. Extreme distal tip of lobes more or less nude (scattered, very minute spines). Stalk of the organ between asulcate spinous portion and spines bordering the sulcus (i.e., the "sides" of the organ) is nude.

The apexes of the lobes of the everted organ were punctured during preparation, but configuration of distal structures was confirmed by examination of the inverted organ of the same specimen. The sulcus extends to the tip of each lobe, which is more or less nude. No peculiar apical structures, as seen in *dolicocercus* and *rhadinæa*, are apparent.

#### The *stumpffi* Group

*Liopholidophis epistibes* (Fully Everted Left Organ of MCZ 180318; Fig. 34).

The organ is deeply bilobed, noncapitate, acalculcate (entirely spinose), with a deeply bifurcate centrolineal sulcus spermaticus. Sulcus spermaticus divides approximately 3 mm from the base of the organ. The lobes diverge strongly from one another, essentially lying at right angles to the stalk. Thus, the distal face of the hemipenis is formed by the surfaces of the lobes that would normally face one another (i.e., the crotch) if the lobes were not so divergent. The tips of the lobes face away from one another at nearly right angles to the axis formed by the crotch and basal stalk. No basal pockets or lobes.

The sulcus spermaticus is a deep groove, bifurcate for about  $\frac{3}{4}$  its length, the branches terminating just short of a central depression at the tip of the lobes. The orientation of the sulcus is therefore centrolineal, even though the lobes themselves diverge at nearly  $180^\circ$  from one another.

The stalk of the organ is very short and ornamented with scattered minute spines. The base of the lobes is encircled by 3-4 rows of enlarged spines on an expanded midsection of the stalk (>30 enlarged spines around base of each lobe); the midsection is set off from the short basal portion of the stalk by a distinct nude shelf. On the sulcate side, the enlarged spines of the midsection approach the sulcus spermaticus at its point of division. On the asulcate side, the spines follow the periphery of the lobes distally, becoming rather abruptly smaller as the lobes turn away from the stalk. The crotch of the organ, including most of the mesial surfaces of the lobes, is nude except for an array of tiny spinules encircling the distal rim of the lobes. The asulcate surface between the lobes is nude, as is a broad expanse of tissue between the spinous midsections.

The distal tips of the lobes have a deep central "umbelliform" depression where the retractor muscle attaches internally (see later). These distal surfaces are ornamented with a sparse array of very tiny spinules, arranged in rather indistinct concentric rows.

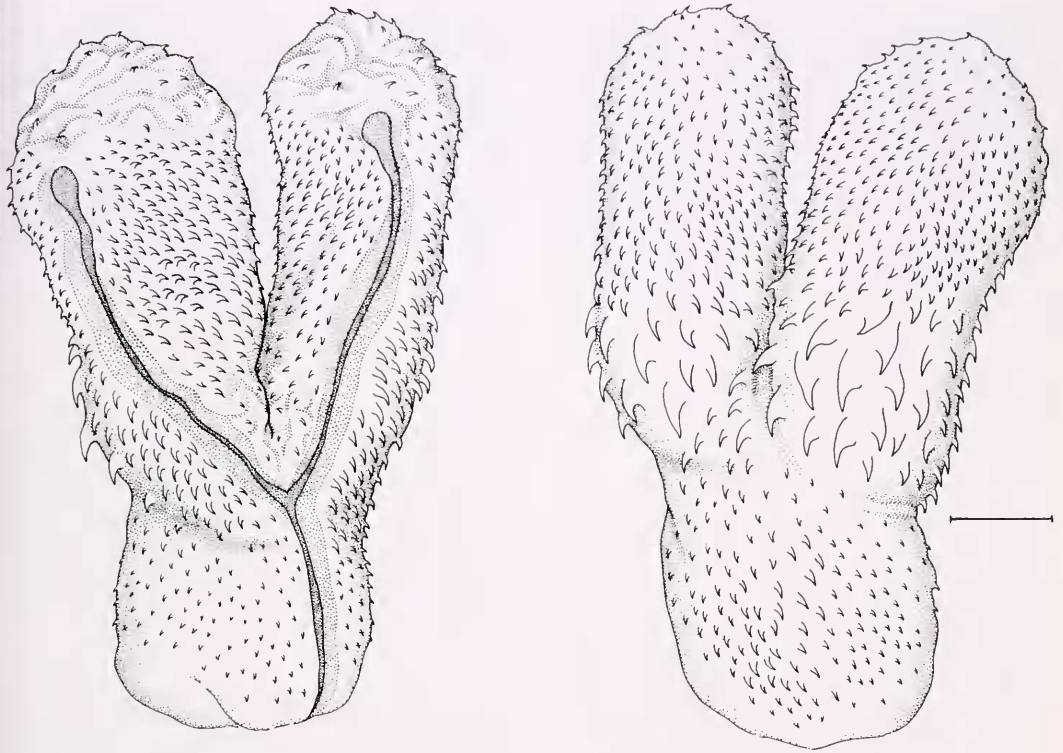


Figure 33. Hemipenis of *Liopholidophis sexlineatus* (Günther). Fully everted organ of MCZ 180333 (from Ambatolahy near the RNP), shown in sulcate (left) and asulcate (right) views. Scale bar = 1 mm.

***Liopholidophis stumpffi*.** The following description is based on the right organ of FMNH 18219, a topotype. The inverted organ was studied superficially *in situ*, before removal and eversion using the method of Pesantes (1994). Although the eversion was successful, the tissue probably is not as expanded as would be an organ everted from a fresh specimen. Thus, although details of ornamentation are easily discernible, the overall shape of the organ, which has rather narrow, unexpanded lobes, would probably be more similar to that described earlier for *epistibes*.

Before removal, the organ extended to the level of the suture between subcaudals 8 and 9, bifurcating at the level of the suture between subcaudals 2 and 3 (hence, having a short stalk and long lobes). The

everted organ is approximately 12 mm total length, bilobed for the distal 9–10 mm (about  $\frac{3}{4}$  bilobed). The sulcus is centrolineal, dividing about 3 mm from the base of the organ. The lobes diverge from one another but may to a greater extent in a naturally everted organ. No basal pockets or lobes. Overall, the organ is deeply bilobed, noncapitate, and acalyculate (entirely spinose), with a deeply bifurcate centrolineal sulcus spermaticus.

The sulcus spermaticus is a deep groove, bifurcate for about  $\frac{3}{4}$  its length, the branches terminating at a central depression at the tip of the lobes on the same side of the organ. The orientation of the sulcus is therefore centrolineal. The distal depression of the lobes would likely assume the “umbelliform” shape seen in other

members of the *stumpffi* group if the lobes attained full expansion. The umbelliform area appears to have scattered minute spines in an otherwise nude area.

The stalk of the organ is very short, ornamented with scattered minute spines. At the base of the lobes, their outer surface has three to four enlarged hooked spines more or less in a curved line around the outer surface. Above the enlarged spines, the outer surface of each lobe is nude for a small area, above which the lobes are ornamented with spines for the distal  $\frac{2}{3}$  of their length. The enlarged spines are separated from the stalk by a nude shelf and a shallow groove. Except in having many fewer enlarged spines, the spinous midsection of the *stumpffi* hemipenis appears similar to that of *epistibes*, although not as expanded as it would probably in a fully inflated organ.

On the sulcate surface, the crotch of the organ has a narrow array of spines bordering the sulcus above its division; otherwise, the crotch is nude on that surface, as well as on the asulcate surface at the base of the lobes. The facing surfaces of the lobes are basally nude (i.e., in the crotch) for about  $\frac{1}{4}$  of its length and spinose for the distal  $\frac{3}{4}$ . These spines are somewhat larger proximally, decreasing in size distally.

*Liopholidophis lateralis*. Domergue (1962:101–102, fig. 13; 1973:1410, fig. 3) briefly described and illustrated hemipenes referred to *Liopholidophis lateralis* but did not indicate the specimens upon which these were based. His two illustrations appear rather different: the earlier figure and description has more strongly divergent and less globose lobes than the later one. Whether this reflects variation or misidentified taxa is unclear (*stumpffi*, *epistibes*, and *thieli* were subsumed within *lateralis* when the 1962 paper was written); the strongly divergent lobes of the organ illustrated in the former paper suggest hemipenes of *L. epistibes*, as already described (but see later summary and comparisons). The *lateralis* hemipenis illus-

trated in 1973 is similar to organs of that species I have studied.

The following description is based on the fully everted right organ of MCZ 180380 (Fig. 35). The organ is deeply bilobed, noncapitate, and acalyculate (ornamentation consists entirely of spines), with a deeply bifurcate centrolateral sulcus spermaticus. Sulcus spermaticus divides approximately 4 mm from the base of the organ. The lobes diverge strongly from one another, creating overall a Y-shaped organ. The tips of the lobes face away from one another at somewhat  $>45^\circ$  angles to the axis formed by the crotch and basal stalk. No basal pockets or lobes. The lobes of this preparation are slightly asymmetrical in size (Fig. 35), but this appears to be subject to some variation, as the left organ of the same specimen and several others examined do not show this asymmetry.

The sulcus spermaticus is a deep groove, bifurcate for about  $\frac{2}{3}$  its length, the branches extending to the tip of the lobes and terminating in a central depression at their distal tips. The thickened lips of the sulcus become closely appressed to one another, especially distally, essentially making a closed channel of the groove below the surface. At the distal end of the sulcus adjacent to the umbelliform depression, the channel of the sulcus spermaticus is  $\geq 1$  mm deep.

The stalk of the organ is short and ornamented with scattered minute spinules. Just proximal to the point of division of the sulcus, the stalk abruptly expands, forming a broad midsection from which the lobes extend. The midsection is set off by a distinct nude shelf from the proximal narrower portion of the stalk. The midsection is arrayed with enlarged hooked spines arranged in clusters: viewed from the sulcate side, a large spine occupies the lower corners of the expanded portion of the stalk, and a cluster of 6–8 medium-sized spines (distally grading into the smaller spines of the lobes) is adjacent to the point of sulcus division; on the asulcate

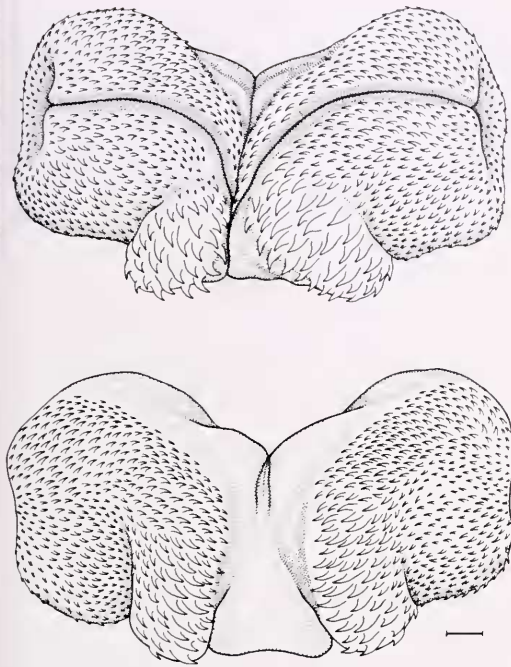


Figure 34. Hemipenis of *Liopholidophis epistibes*, new species. Fully everted organ of MCZ 180318 (from Talatakely in the RNP), shown in sulcate (top) and asulcate (bottom) views. The distal "umbelliform" tips to the lobes in the sulcate view appear to be normal features, rather than a result of incomplete eversion (see text: "Summary and Comparisons of Hemipenes of *Liopholidophis*"). Scale bar = 1 mm.

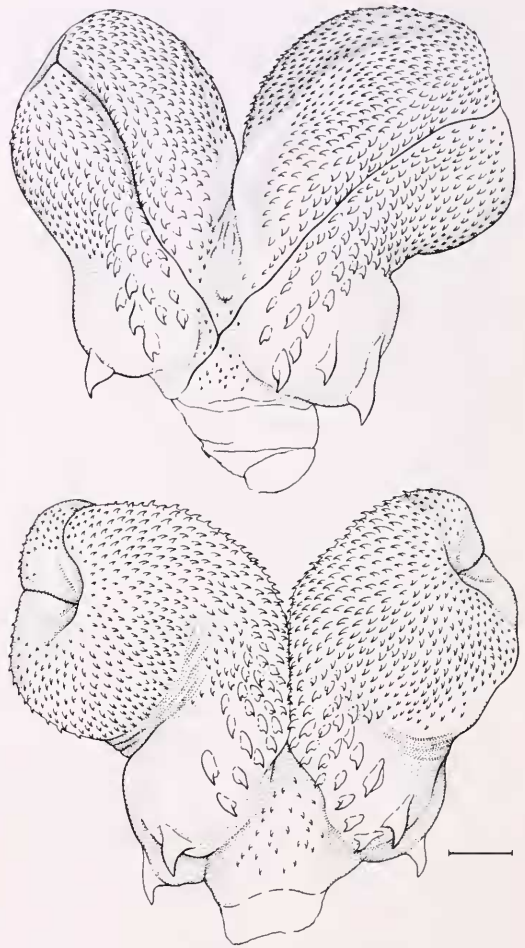


Figure 35. Hemipenis of *Liopholidophis lateralis* (Duméril, Bibrón, and Duméril). Fully everted organ of MCZ 180380 (from near Midongy du Sud), shown in sulcate (top) and asulcate (bottom) views. The distal "umbelliform" tips to the lobes appear to be normal features, rather than a result of incomplete eversion (see text: "Summary and Comparisons of Hemipenes of *Liopholidophis*"). Scale bar = 1 mm.

side the midsections bear 10–12 enlarged hooked spines (larger proximally, smaller distally) that grade into the small spines on the lobes. Large areas of nude tissue occupy the midsections between the clusters of spines.

A few small spines are present in the fork of the sulcus. Small spines and spinules ornament the lobes except the nude central depression at their distal tips; a small wedge of nude tissue is in the crotch of the organ and adjacent basal facing portions of the lobes, forming a continuous stretch of nude tissue in the crotch between the asulcate and sulcate sides (i.e., the spinous areas of the lobes are not continuous with one another across the crotch).

As the lobes diverge from one another, their distal ends turn slightly toward the

asulcate surface, so that more of the tips of the lobes is visible from the asulcate than from the sulcate side. Lobes, except for the distal depression, are entirely ornamented with small spines, which are larger proximally. The distal tips of the lobes are nude and have a deep central depression (described as "umbiliform" by Domergue, 1962:101) where the retractor muscle attaches to the inside of the lobes.

*Liopholidophis infrasignatus*. Domergue (1973:fig. 8) illustrated an everted hemipenis of *infrasignatus* ("thieli"). The following description is based on the fully everted right organ of MCZ 180368 (Fig. 36). The organ is deeply bilobed, noncapitate, and acalyculate (entirely spinose), with a deeply bifurcate centrolineal sulcus spermaticus. Total length approximately 15 mm, bilobed for the distal 4 mm. Sulcus spermaticus divides approximately 6.5 mm from the base of the organ. The lobes diverge slightly, and their distal tips face away from one another (see comments in later summary and comparisons). No basal pockets or lobes are present.

The sulcus spermaticus is a deep groove, bifurcate for somewhat more than  $\frac{1}{2}$  its length, the branches extending to the tip of the lobes and terminating in a central umbelliform depression.

The organ has a narrow stalk ornamented with scattered small spines and an abruptly expanded midsection proximal to each lobe. The expanded midsections have a battery of enlarged, hooked spines (15–20 on each midsection) more or less evenly distributed around the circumference of the organ. These spines are larger on the sulcate than the asulcate side, arranged roughly into two to three rows, and grade into the smaller spines of the lobes. On the asulcate side, the spinous midsections of either side are separated from one another by a nude gap in the crotch. The enlarged spines are separated by a shelf of nude tissue and a distinct groove (most prominent on the asulcate side) from the spinous stalk. The spines of the midsection grade into those of the lobes on the "lateral" surfaces of the organ, with an abrupt size transition at the juncture of the lobes and midsections.

The distal tips of the lobes have a deep central "umbelliform" depression. The lobes are ornamented with minute spines except distally, where a band of nude tissue encircles the umbelliform depression, and proximally in the crotch of the organ. Except for several minute spines within

the fork of the sulcus spermaticus, the crotch of the organ is nude from the sulcus spermaticus to the spinous stalk on the asulcate side. The inner surfaces of the lobes (i.e., facing the crotch) are also nude except for a spinous band encircling the distal tips of the lobes (occupying the distal 15–25% of the facing surfaces of the lobes).

#### Summary and Comparisons of Hemipenes of *Liopholidophis*

Hemipenial morphology in the *sexlineatus* group is more heterogeneous than in the *stumpffi* group. Relative to body size, three species (*grandidieri*, *rhadinaea*, *sexlineatus*) have rather small organs, whereas *pinguis* is intermediate in size, and *dolicocercus* is large. *Liopholidophis dolicocercus*, *L. rhadinaea*, and *L. sexlineatus* have peculiar apical structures that are quite different from one another; the others have no such structures. The hemipenes of *sexlineatus* and *grandidieri* are the most similar pair in size and details of ornamentation (Figs. 32–33), but these are the most generalized organs of the series, lacking any especially distinctive features except for the spinose papillae on the lobes in *sexlineatus*.

In comparison to the *sexlineatus* group, hemipenes of species of the *stumpffi* group are more homogeneous but quite different from those of the *sexlineatus* group. Hemipenes of the *stumpffi* group have a relatively short basal stalk (essentially none in *epistibes* and *stumpffi*) compared to those of the *sexlineatus* group. The organ is about  $\frac{1}{3}$  bilobed in *infrasignatus*, about  $\frac{1}{2}$  bilobed in *lateralis*, and much more than  $\frac{1}{2}$  bilobed in *epistibes* and *stumpffi*. Hemipenes in the *sexlineatus* group are about 50% or less bilobed (greatest in *dolicocercus*), and all species in this group have a prominent stalk. The organs of the *stumpffi* group are also large relative to body size compared to all species of the *sexlineatus* group except *dolicocercus*.

Within the *stumpffi* group, the hemipenes of *stumpffi* and *epistibes* are more similar to one another in having a very



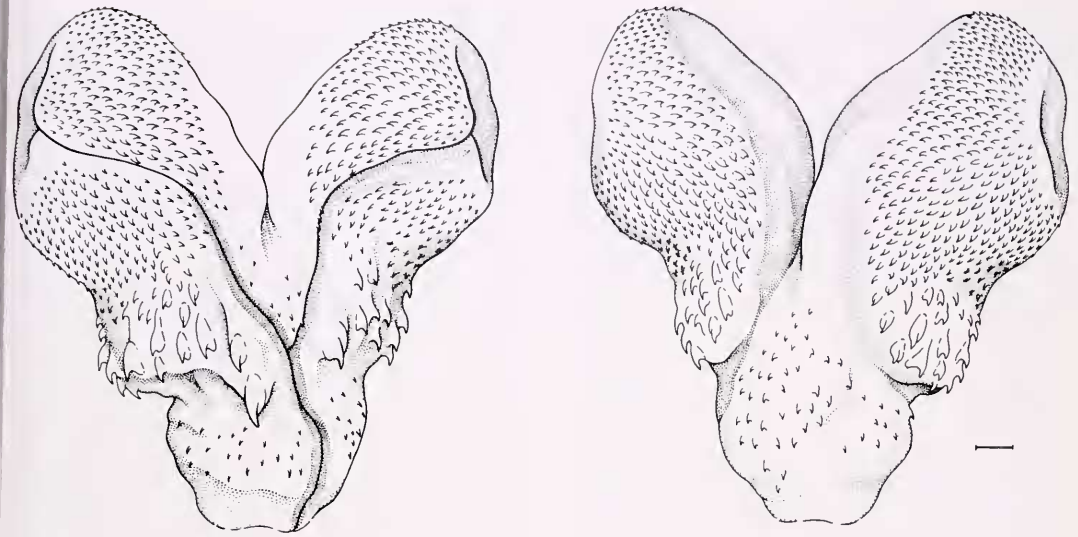


Figure 36. Hemipenis of *Liopholidophis infrasignatus* (Günther). Fully everted organ of MCZ 180368 (from Talatakely in the RNP), shown in sulcate (left) and asulcate (right) views. The distal "umbelliform" tips to the lobes in the asulcate view appear to be normal features, rather than a result of incomplete eversion (see text: "Summary and Comparisons of Hemipenes of *Liopholidophis*"). Scale bar = 1 mm.

reduced stalk, whereas *lateralis* and *infrasignatus* have organs of more typical proportions; the former condition is considered derived (see following section). On the other hand, the organs of *stumpffi* and *lateralis* are similar in having few enlarged spines on the midsection, whereas *infrasignatus* and *epistibes* have many enlarged spines in this area (cf. Table 3).

The overall form of the hemipenis of *epistibes*, with its lobes widely diverging so that the "crotch" of the organ actually forms its distal face, appears unusual but may be at least partly influenced by internal attachment and constraint by the retractor muscles. Such an effect is suggested by comparison of the organ of *infrasignatus* previously described with its partner, which was inflated with jelly while still attached to the specimen. The *infrasignatus* organ described earlier had lobes only slightly diverging, whereas its partner is similar to *epistibes* in having the lobes much more widely diverging.

Hemipenes of the *stumpffi* group are characterized by two unusual features that are discussed separately here.

(1) Presence of an "umbelliform" depression at the tip of the lobes. At first the depression appears to result from incomplete inflation of the hemipenis. However, it is a consistent feature of the hemipenes of all specimens of *epistibes*, *lateralis*, and *infrasignatus* I prepared in the field, despite a conscious effort to effect greater eversion. That the distal depression is not an artifact was proved by internal dissection of an everted organ of *L. lateralis* (MCZ 180347). The dissection revealed that the "dimpled" appearance results from broad internal attachment of the *M. retractor penis magnus* to the somewhat pleated tissue at the tip of the lobes. No "uneverted" tissue appeared to remain inside the organ, and I conclude that the umbelliform structure is a normal feature of these organs.

The umbelliform lobes of the *stumpffi*

group are unusual among colubrid hemipenes and here interpreted as a synapomorphy of the group (see "Monophyly of the Species Groups of *Liopholidophis*"). However, similar structures appear in hemipenes of some species of *Liophidium* (personal observations of *Liophidium rhodogaster*, and a description and illustration of the organ of *Liophidium vaillanti* ["L'apex . . . avec une dépression centrale" and fig. 5B in Domergue, 1983]). As already alluded to (description of *rhadinæa*), and as will be revisited later, generic limits of these and other Malagasy colubrids need reevaluation (see "Monophyly of *Liopholidophis*" and the discussion of MNHN 1988-331). Proper phylogenetic interpretation of the umbelliform lobes of the *stumpffi* group will only be possible with a broader survey of hemipenial morphology of other Malagasy colubrids. Nevertheless, the unusual nature of the umbelliform lobes in hemipenes of the *stumpffi* group are reasonably interpreted as a synapomorphy of the group at present.

(2) An expanded midsection of the hemipenial stalk, set off by a nude shelf and/or groove from the narrow basal portion of the stalk (less distinctly differentiated from the lobes). In the *stumpffi* group, the enlarged spines encircling the base of the lobes occupy this expanded midsection. Among other Malagasy colubrid hemipenes examined (representatives of *Geodipsas*, *Liophidium*, *Lycodryas*, *Mimophis*, *Dromicodryas*, *Madagascarophis*, and *Pseudoxyrhopus*), only *Pseudoxyrhopus tritaeniatus* had a expanded midsection somewhat similar to that in the *stumpffi* group. However, in *P. tritaeniatus*, the midsection is not as distinctly set off as in members of the *stumpffi* group. Because of the seemingly restricted taxonomic distribution of a differentiated spinose hemipenial midsection, I interpret this feature as a synapomorphy of the *stumpffi* group. Within the *stumpffi* group, a differentiated midsection seems least developed in *stumpffi* (although this interpretation is perhaps influenced by the ever-

sion method of the organ studied; see earlier) and best developed in *infrasignatus* and *lateralis*. The midsection is not discrete in organs that are not well inflated and is easily overlooked, for example, in everted organs that are nonetheless flaccid.

In hemipenes of the *stumpffi* group, the nude shelf and/or groove delimiting the midsection is reminiscent of the overhanging shelf setting off the capitulum of those Neotropical colubrid hemipenes described as "capitate" ("xenodontines" *sensu lato*; see Myers, 1973:30-31, 1974:31; Myers and Campbell, 1981:15-17; Myers and Cadle, 1994:13-14). However, the capitation observed in the latter organs does not appear homologous with the condition seen in the *stumpffi* group,<sup>13</sup> as suggested by two features: (a) the midsection of hemipenes in the *stumpffi* group is set off by a less well-defined groove and shelf than is the capitulum in truly capitate organs, and (b) in truly capitate organs, the groove delimits a distinct, distal "capitulum" in the case of non-bilobed organs or, in bicapitate or semicapitate organs, a capitulum on each hemipenial lobe (in which case the overhang delimiting the capitulum is considerably distal to the division of the sulcus spermaticus). The differentiated midsection of hemipenes in the *stumpffi* group appears more closely associated with the stalk of the hemipenis, rather than with the lobes, and the delimiting groove and shelf are proximal to the division of the sulcus spermaticus.

One other feature of all hemipenes of *Liopholidophis* seems worthy of note. In comparison to a wide variety of other colubrids, the sulcus spermaticus of hemipenes of *Liopholidophis* seems unusually broad and deep, although I have been unsuccessful in quantifying the variation. In many colubrids, the sulcus spermaticus has

<sup>13</sup> Some forms of capitation in Neotropical colubrids also have apparently been independently derived more than once. See Myers and Cadle (1994: 13-14 and references therein) for discussion.

a narrow opening on the surface of the hemipenis, is bordered by a very narrow (sometimes indistinct) lip, and appears as a line on the surface of the organ. In *Liopholidophis* (all species of both species groups), the sulcus has a broad surficial opening and is bordered by thickened lips; it appears as a deep, open trough except in some cases (as in *lateralis*, described earlier) in which the lips are appressed to one another and essentially form a closed canal. No similar structure was observed in hemipenes of other Malagasy colubrids, with the exception of several *Geodipsas* spp., which otherwise have quite different hemipenes from *Liopholidophis*. I offer neither a functional nor systematic interpretation of the unusual sulcus structure here but call attention to this apparently variable feature of colubrid hemipenes, which seems not to have been previously reported.

#### OSTEOLOGICAL COMPARISONS

I have examined one skull each of the species *dolicocercus*, *grandidieri*, *pinguis*, and *rhadinaea*, and two skulls each of *epistibes*, *infrassignatus*, *lateralis*, and *sexlineatus* (Appendix). I have not seen a skull of *stumpffi*, and where I generalize to *Liopholidophis sensu lato* or to the *stumpffi* species group later, I am assuming that the characteristic under consideration is similar in *stumpffi* as in other species of its group (for species group characters) or for the genus as a whole (other characters). This should present no problem, as the skulls of the other species are rather homogeneous for those characters at the appropriate level of comparison.

A complete osteological description is not attempted here. I discuss only some salient characteristics of the genus; skull characters differentiating the species groups are presented in a later section (see "Monophyly of the Species Groups of *Liopholidophis*"). Polarization of character states as primitive and derived is, in most cases, impossible without reference to an explicit series of outgroups, a hierarchy

unavailable with present knowledge of Malagasy colubrids.

*General Features of the Skulls of Liopholidophis.* Skulls of all species of *Liopholidophis* are lightly built and of rather ordinary colubrid proportions (Figs. 38–40). Prefang maxillary teeth moderate in number in the *sexlineatus* group (17–26;  $\bar{x}$  = 20–24) and in *infrassignatus* ( $\bar{x}$  = 22); higher in *stumpffi*, *epistibes*, and *lateralis* (22–31, averaging >25 in each species) (Tables 1–2).

*Orbital Region.* The frontals and parietal are considerably emarginated in all species, forming a large orbital foramen (Fig. 40); hence, the ventral borders of the frontals and parietal are widely separated below the orbital foramen. In the *stumpffi* group, the ventral and posteroventral edges of the frontals are emarginated to a greater extent than in the *sexlineatus* group. Consequently, in the *stumpffi* group the frontals rest on a high frontal crest of the sphenoid (Fig. 40; see later); the frontals are less emarginated ventrally and the frontal crest of the sphenoid is more poorly developed in the *sexlineatus* group (Fig. 40). Ventral emargination of the frontals similar to that of the *stumpffi* group and associated features such as a high frontal crest on the sphenoid were observed also in *Dromicodryas*, but not in the other Malagasy colubrid skulls examined. The trabecular groove is open along its entire length and is not obscured laterally by an overlapping flange of the frontal.

*Basiscranial and Posterior Cranial Regions.* The Vidian canals are of moderate length (see Myers and Cadle [1994: footnote 9] for notes concerning terminology of Vidian canals). The anterior Vidian foramen is well inside the border of the sphenoid and lies immediately anterior to a bony ridge on the basisphenoid. Detailed morphology of the sphenoid differs between the two species groups, and those differences are described later. Trigeminal foramina double on each side, separated by flange of prootic. A pair of sympathetic foramina on each side ventral to trigeminal foramen.

## PHYLOGENETIC RELATIONSHIPS

### Monophyly of *Liopholidophis*

There appears to be no unequivocal synapomorphy of *Liopholidophis sensu lato*, which was characterized by Mocquard (1904:303–304) as follows:

Maxillary teeth in continuous series, about 20 to 25; mandibular teeth subequal, decreasing gradually in length from front to back; head more or less distinct from the neck; eye moderately developed, with round pupil; body cylindrical; tail usually much longer in males than in females; scales smooth, without apical pits, in 17 or 19 longitudinal series; ventrals without lateral keel; anal and subcaudals divided; posterior trunk vertebrae bearing hypapophyses; hemipenis strongly bifurcate.

Mocquard's (1904) erection of *Liopholidophis* resulted from his discovery that these Malagasy colubrids had a deeply bifurcate hemipenis, in contrast to most species of *Tropidonotus*, where these species had been placed by Boulenger (1893). Boulenger (1893, 1915) had maintained the then-recognized species in the large genus *Tropidonotus* Kuhl (section *Amphiesma*; Boulenger, 1893:197), apparently based on their possession of hypapophyses on the posterior trunk vertebrae, but otherwise of rather generalized colubrid morphology (i.e., lacking "derived" features of other hypapophysiate Madagascan genera, such as enlarged anterior mandibular teeth in *Dromicodryas*). Parker (1925) and subsequent authors (Werner, 1929; Guibé, 1954, 1958; Domergue, 1973; Glaw and Vences, 1992, 1994) used Mocquard's concept of *Liopholidophis*.

Indeed, other than the elongate tails of males, which pertains to only a subset of species, *Liopholidophis* has been a repository for generalized, diurnal, smooth-scaled Malagasy colubrids lacking characters such as grooved rear fangs (all Malagasy colubrid genera except *Dromicodryas*, *Leioheterodon*, *Liophidium*, *Liopholidophis*, and *Micropisthodon*), enlarged mandibular teeth (e.g., *Dromicodryas*, *Micropisthodon*, *Pseudoxyrhopus*), rostral modifications (e.g., *Leioheterodon*), vertical pupils (e.g., *Madagascarophis*), or mandibular and

dental modifications (e.g., *Liophidium*). This situation, in conjunction with external and internal morphological characters differentiating the two species groups (see later), strongly suggests the possibility of paraphyly (or even polyphyly) of *Liopholidophis*. However, there seems little point in altering the composition of the genus until broader relationships among Malagasy colubrids are examined. Until such time, Mocquard's (1904) definition of *Liopholidophis* need only be modified to reflect the fact that the tail is unusually elongate in males of only a section of the genus (*sexlineatus* group) and that these snakes otherwise lack the distinguishing features (? putative synapomorphies) of other Malagasy genera, as just noted. Nevertheless, the uncertain monophyletic status of *Liopholidophis* requires independent treatment of the two species groups (which, as documented later, appear to be monophyletic) in comparative or phylogenetic analyses involving Malagasy colubrids. The content of *Liopholidophis* should be reevaluated as the morphology and relationships of Madagascan colubrids becomes better understood.

### Monophyly of the Species Groups of *Liopholidophis*

Parker (1925) recognized two species groups of *Liopholidophis* based on two "key" characters: the *sexlineatus* group characterized by 17 midbody scale rows and the elongate tail of males, including *sexlineatus*, *dolicocercus*, and *grandidieri*, and the *stumpffi* group characterized by 19 midbody scale rows and the tail in males of "normal" proportions, including *stumpffi* and *lateralis*. Parker (1925) left *L. pinguis*, which has 17 scale rows but "normal" tail proportions (but see later), unplaced as to species group.

I retain Parker's (1925) species groups, but their composition is changed to reflect subsequent new species and revisions (Domergue, 1973, and herein). Furthermore, I consider each a monophyletic clade, notwithstanding lack of supporting evidence

for monophyly of *Liopholidophis sensu lato*. Thus, the *sexlineatus* group includes *dolicocercus*, *grandidieri*, *pinguis*, *rhadinaea*, and *sexlineatus*; the *stumpffi* group includes *infrassignatus*, *lateralis*, *epistibes*, and *stumpffi*. Species of the two groups are easily distinguished by multiple characters, including tail sexual dimorphism, dorsal scale row number, and skull and hemipenial morphology. The *sexlineatus* group is supported by several apparent synapomorphies, whereas synapomorphies supporting the *stumpffi* group are fewer in number and more equivocal. However, species in the *stumpffi* group are similar to one another in external and (especially) hemipenial morphology. I here document the distinguishing characteristics of these groups and include an amplified discussion of several characteristics (e.g., tail length differences). Hemipenial characters are discussed more fully in the previous section.

Apparently derived characteristics are indicated by "D" and the rationale for considering them derived is given. Other characters will not be polarizable until additional Malagasy colubrids are more comprehensively studied. In assessing taxonomic distribution of several characters, I draw on personal observations from a wide variety of colubrids (especially Neotropical). In addition to skulls of *Liopholidophis* (see the Appendix for listing), I examined skulls of the following Malagasy colubrids: *Dromicodryas bernieri* (JEC 12595, 12632), *Geodipsas infralineata* (JEC 11815), *Langaha nasuta* (MCZ 18017), *Leioheterodon modestus* (MCZ 177382), *Liophidium torquatum* (MCZ 11572) and *L. rhodogaster* (JEC 11571), *Lycodryas betsileanus* (JEC 11839), *Mimophis mahfalensis* (MCZ 11715), and *Pseudoxyrhopus tritaeniatus* (JEC 11716) (JEC specimens to be cataloged in the MCZ). A few skull characters were discernible for several species of *Liophidium* from figures or descriptions in Morgan (1973). Numbered characters correspond under the headings for each species group, and present contrasting characteristics for the two groups.

**The *sexlineatus* Species Group.** All species of the *sexlineatus* group share the following characters:

(1) 17 scale rows at midbody.

(2, D) Strong sexual dimorphism in relative tail length (tail length as a percentage of total length). The difference between means for males versus females ranges from 7% in *pinguis* to 20% in *grandidieri* (1–2% in species of the *stumpffi* group; Fig. 37). Expressed differently, the total ranges of relative tail length in males and females do not overlap in any species of the *sexlineatus* group, whereas, although males tend to have longer tails in species of the *stumpffi* group, the sexes broadly overlap in their ranges of tail proportions (the usual situation in colubrids). When the overlap is expressed as [minimum ♂ value minus maximum ♀ value], the difference ranges from 4 to 29% in the *sexlineatus* group and negative values 1 to 3% in the *stumpffi* group (Fig. 37). Additional sampling of *pinguis* will possibly reveal less distinction between males and females of this species, in which case the extreme sexual dimorphism in tail length would be a synapomorphy of only the section of the *sexlineatus* group including *dolicocercus*, *grandidieri*, *rhadinaea*, and *sexlineatus*. A hypothesis for relationships among species put forward below suggests this as a possibility.

As is apparent from Figure 37, the distinctiveness of the tail proportions in the *sexlineatus* group is attributable to the extraordinary lengths of tails in males of *dolicocercus*, *grandidieri*, *rhadinaea*, and *sexlineatus*. Females of these species, as well as both sexes of other species of *Liopholidophis*, are rather ordinary in proportional tail length. Ironically, as the tails of males of the *sexlineatus* group are produced to extraordinary lengths, the tails of females (except *grandidieri*) revert to relatively shorter lengths in comparison to those of the *stumpffi* group (Fig. 37).

Comparable data on relative tail length differences for other colubrids are widely scattered, but I am aware of no other species in which the sex differences approach

those of the *sexlineatus* group. One compilation for 16 Neotropical colubrids revealed, for two species, maximum differences of 6% between means of proportional tail length for each sex; the modal value for the 16 species was 1% difference (Guyer and Donnelly, 1990:table 3). Two colubrids in that study with tail lengths >40% total length (*Oxybelis aeneus* and *Rhadinaea decorata*) showed typical overlap in ranges of proportional tail length between the sexes (means for each sex were identical in *O. aeneus*; cf. also Myers, 1974: 59, 70, for *R. decorata*). Klauber (1943) reported similarly narrow differences in relative tail lengths between males and females of a wide variety of North American colubrids. Clearly, species of the *Liopholidophis sexlineatus* group are unusual, perhaps unique among colubrids, in this regard.

The sexual dimorphism in tail length and subcaudal number in the *sexlineatus* group is presumably apparent at hatching or birth, but I have seen few specimens of that size, and all those were females, as determined by examination of gonads or for hemipenes. These included three near-hatchlings of *rhadinæa* (MCZ 180387–88, 180398; SVL 122–170 mm) and one of *sexlineatus* (MCZ 180378; SVL 180 mm). The smallest males of *rhadinæa* (MCZ 180396, 180402; SVL 281 and 245 mm, respectively), *sexlineatus* (MCZ 11606; SVL 259 mm), and *dolicocercus* (MZUT 796; SVL 265 mm; data from Peracca, 1892) are either at or toward the lower end of the ranges of proportional tail length for males of those species (Fig. 37). On the other hand, their subcaudal counts are toward the higher ends of the ranges for their respective species. These observations suggest only a weak association between subcaudal count and relative tail length, as well as an increase in relative tail length with growth in these species. Although seemingly counterintuitive, correlations between tail length and subcaudal counts are weak in several species of colubrids (Klauber, 1945; see also Arnold and Bennett, 1988).

One might expect the longer tails of species in the *sexlineatus* group to incur greater frequency of breaks than those of the *stumpffi* group or greater frequency of breakage of the long tails of males in the former group compared to females. Neither expectation holds: species of the *sexlineatus* group do not show greater frequency of tail breakage than those of the *stumpffi* group. Moreover, only in *lateralis*, in which males do not have inordinately long tails, and *sexlineatus*, were most specimens with tail breaks males. Percentages of specimens with healed breaks were as follows (percentage followed by total sample size and proportion of specimens with breaks that were male): *dolicocercus* (0%, 9), *grandidieri* (25%, 4, 0/1), *pinguis* (25%, 12, 0/3), *rhadinæa* (5%, 19, 1/1), *sexlineatus* (10%, 30, 3/3); *infrasinatus* (20%, 32, 1/5), *lateralis* (20%, 44, 7/10), *epistibes* (4%, 24, 0/1), and *stumpffi* (0%, 13).

(3, **D**) *Male superiority in body size (SVL) and ventral counts.* With the exception of *dolicocercus*, males of species in the *sexlineatus* group reach greater maximum SVLs than do females (Table 1). The absence of this trend in *dolicocercus* is probably due to the small sample of males (5) of that species, and I predict its occurrence in *dolicocercus* when sufficient samples are available. Males are nearly 40% greater in maximum SVL than females in *rhadinæa* and *sexlineatus*, the two species with reasonable samples of both sexes (Table 1).

Perhaps associated with superior male size in species of the *sexlineatus* group, males of this group (including *dolicocercus*) also have higher ventral counts than females (Table 1). In all species, ranges for ventral counts show virtually no overlap between the sexes, and means for the sexes differ by 8–18 ventrals. As with the statistical correlation between tail length and subcaudal number, Klauber (1945) was unable to demonstrate significant correlation between body length and ventral number.

Female superiority in body size and

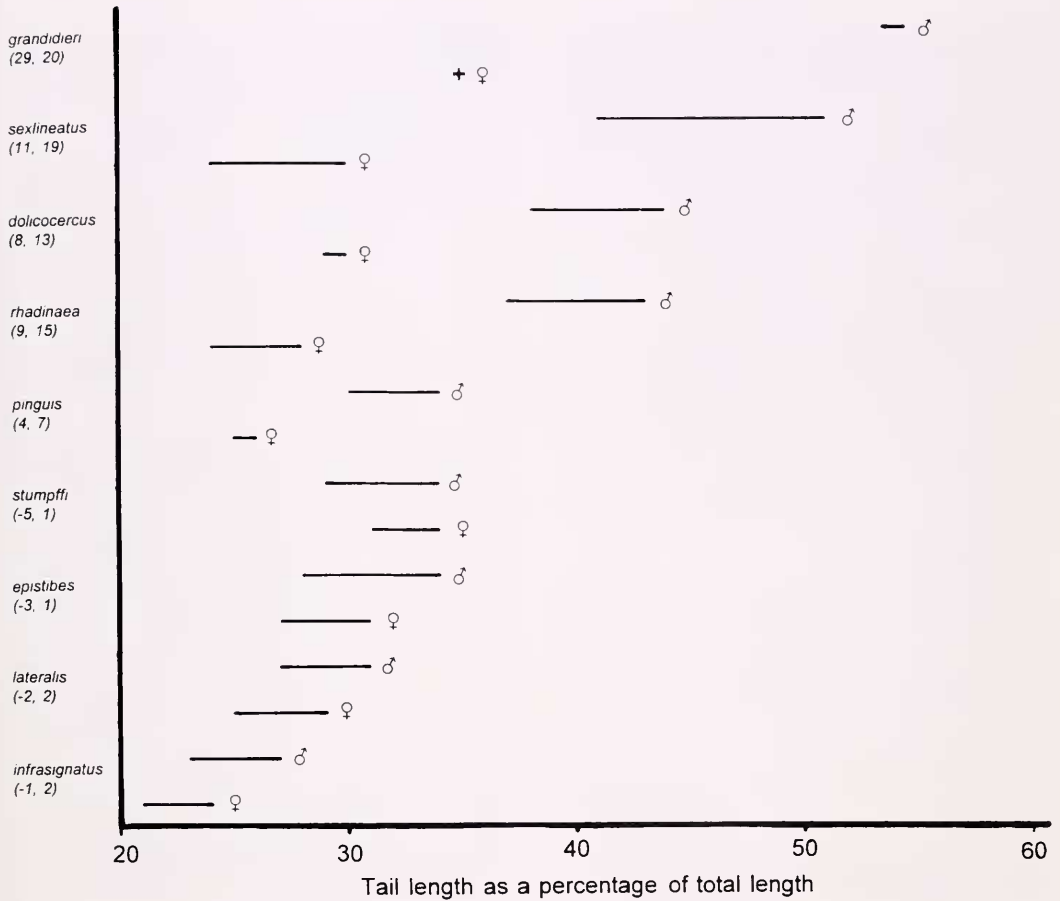


Figure 37. Distribution of tail lengths as a percentage of total lengths in species of *Liopholidophis* (horizontal axis). Bars indicate the total range of percentages for each species, separated by sex. Numbers within parentheses under each species name indicate, respectively, (a) the difference (%) between the minimum male value and maximum female value; and (b) the difference between the mean values for males and females (%).

ventral counts is the rule in the *stumpffi* group (Table 2), as it is in most colubrids (see, e.g., tabulation in Shine, 1991; notable exceptions occur among garter snakes [*Thamnophis*] and their relatives, as discussed by Arnold, 1988, and Arnold and Bennett, 1988). Based on the infrequent occurrence of male size superiority in colubrids, this character is considered a synapomorphy of the *sexlineatus* group. Given the nonsignificant correlation between ventral counts and body size in snakes (Klauber, 1945), the former could perhaps be considered as a separate, corroborating

synapomorphy, although conservatively not treated so here.

(4, **D**) *Contact or virtual contact between the postorbital and frontal* (Fig. 38). The postorbital nearly contacts the frontal in all species of the *sexlineatus* group; occasionally, the three bones more or less form a three-way junction. Based on examination of a wide variety of other colubrids, this character seems to appear most often in species known or suspected to be at least partly semifossorial or in diminutive leaf-litter snakes. Its occurrence in terrestrial snakes such as species of the

*sexlineatus* group is considered derived. Among other Malagasy colubrids, this state is observed in *Pseudoxyrhopus tritaeniatus* and species of *Liophidium* (*mayottensis*, *rhodogaster*, and *vaillanti* fide Morgan, 1973:figs. 25–27; personal observations of *rhodogaster* and *torquatum*), but not in species of *Mimophis*, *Dromicodryas*, *Langaha*, *Leioheterodon*, *Lycodryas*, *Geodipsas*, or the *Liopholidophis stumpffi* group (postorbital and frontal widely separated in these snakes).

(5, D) *Anterior end of the sphenoid narrow, ending in a single point* (Fig. 39).

(6, D) *Lateral margins of the cultriform process of the sphenoid convergent, forming a narrow isosceles triangle extending forward from the basal part of the bone* (Fig. 39).

Characters (5) and (6) are uniformly present in species of the *sexlineatus* group, giving the sphenoid of these snakes an unusual form. *Pseudoxyrhopus tritaeniatus* and *Liophidium* spp. also have a triangular sphenoid with a single point anteriorly, but details of shape differ from those of the *sexlineatus* group. (Morgan [1973] reported the sphenoid as “notched” anteriorly in *Liophidium rhodogaster*, but it had a single point in the specimen I examined.) No other Malagasy colubrids examined had a similar configuration. States (5) and (6) in the *sexlineatus* group are similar to those in Neotropical snakes of the tribe Pseudoboini and to burrowing snakes of many clades. However, they are unusual among fully terrestrial colubrids and, consequently, considered apomorphic states of the *sexlineatus* group.

(7) *Ventral surface of the sphenoid anterior to the anterior Vidian foramina bears a deep median groove*. The anterior median portion of the basisphenoid, more or less between the anterior Vidian foramina, bears a bulbous protuberance. The groove referred to extends forward from this protuberance and is between a pair of parallel bony ridges extending along the cultriform process of the sphenoid. The groove is deepest posteriorly (next to the

protuberance); the bony ridges and the groove itself become less prominent anteriorly. Although species of the *stumpffi* group have a similar median protuberance on the sphenoid, no bony ridges or associated groove occur in species of this group; instead, the sphenoid is flat or even slightly convex in this region (a very shallow groove is present in the two skulls of *lateralis* examined but was not bordered by bony ridges). *Pseudoxyrhopus tritaeniatus* and *Geodipsas infralineata* also have a broad groove on the anterior portion of the sphenoid.

(8) *Ventral border of frontal usually contacting the dorsal margin of the trabecular grooves for well more than half the length of the ventral edge of the frontal* (Fig. 40). This character state is most extreme in *dolicocercus*, *pinguis*, and *rhadinaea*, in which the entire ventral edges of the frontals parallel the dorsal border of the trabecular grooves; in these species, the sphenoid bears only a slight indication of a frontal step. In *sexlineatus* and *grandidieri*, the posteroventral edge of the frontals is emarginated and supported on a short frontal step of the sphenoid; in these species, the posteroventral border of the frontals forms an angle  $<30^\circ$  with the dorsal margin of the trabecular grooves (cf. *stumpffi* group).

(9) *Dorsal plate of frontals, viewed as a unit, about as wide at its narrowest point as its length* (Fig. 38). Species of the *sexlineatus* group have a more or less squarish shape to the paired frontals, contrasted with the more rectangular shape seen in the *stumpffi* group. Thus, the interorbital portion of the dorsal plate of the frontals is relatively wide (Fig. 38).

(10) *Dark stripe occupying at least the lower portion of the first dorsal scale row (usually also occupying the suture line with the ventral scutes and the outer portion of the ventrals)*. In *rhadinaea*, the stripe is brown and generally restricted to dorsal row 1 (general darkening of the flanks in the “dark” morph extends to outer edges of the ventrals); in the other spe-



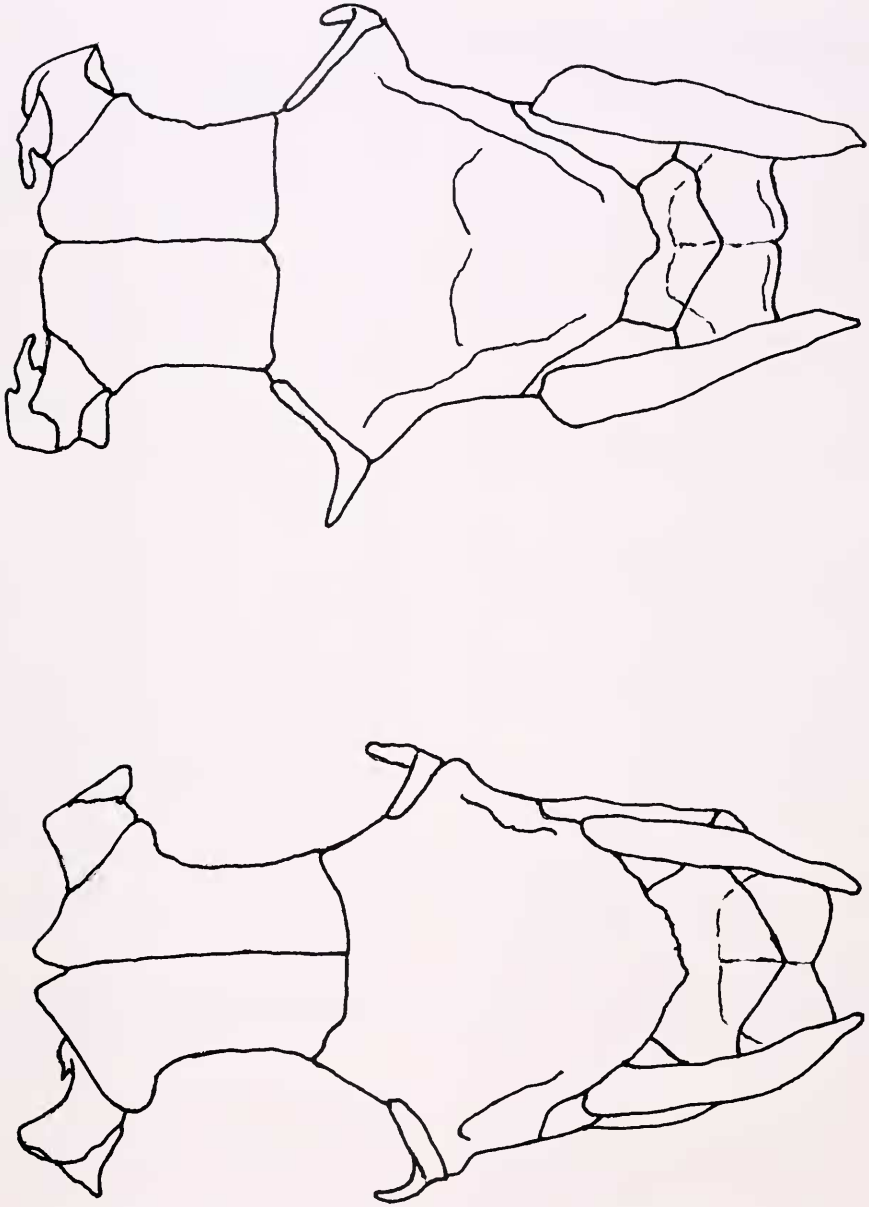


Figure 38. Dorsal views of skulls of *Liopholidophis* showing differences between the *sexlineatus* and *stumpffi* groups (represented by *dolicercus* and *lateralis*, respectively). Top: *L. doliocercus* (MCZ 180409). Bottom: *L. lateralis* (MCZ 180350). See text for discussion.

cies, the stripe is black, usually involves the adjacent venter (often substantially so in *sexlineatus*), and sometimes involves other dorsal rows. In *pinguis*, the stripe is

indistinct anteriorly, often restricted to the suture line between ventrals and dorsal row 1. The stripe is well developed in *dolicercus* and *grandidieri*. No such discrete

stripe is present in species of the *stumpffi* group, although lateral edges of the ventrals may be spotted or stippled.

(11) *Dorsolateral light stripe*. Absent in all species of the *sexlineatus* group except *rhadinæa* (universally present in *stumpffi* group). Some specimens of *Liopholidophis sexlineatus* appear to have light dorsolateral stripes (e.g., Glaw and Vences, 1994:pl. 348), but this results from the generally dark middorsum and flanks, rather than from presence of a discrete dorsolateral light stripe.

(12) *Apical pits absent*. Apical pits are absent in all species of the *sexlineatus* group, whereas they are present in species of the *stumpffi* group.

(13) *Passive defense*. Species of the *sexlineatus* group normally seem to use no special defenses such as biting or neck/body flattening (see species accounts; cf. *stumpffi* group).

(14) *Apical ornamentation of hemipenes various, but never "umbelliform."* See hemipenial descriptions and compare *stumpffi* group.

(15) *Undivided portion of hemipenis (stalk) well developed*. The stalk is approximately 40–50% or more the total length of the hemipenis in the *sexlineatus* group. This state is probably plesiomorphic given its wide distribution in taxonomically diverse colubrids, but equivocally so given the lack of explicit outgroups for these snakes.

(16) *Stalk of hemipenis not differentiated into a narrow proximal portion and an expanded midsection that is set off from the proximal portion by a nude shelf and/or delimiting groove*. See hemipenial descriptions and compare *stumpffi* group.

**The *stumpffi* Species Group.** The *stumpffi* species group is characterized by the following characters (additional commentary on some characters in the section immediately preceding; numbered characters in the two sections correspond):

(1) *19 midbody scale rows*.

(2) *Relative tail length not strongly sexually dimorphic (Fig. 37)*.

(3) *Female superiority in body size (Table 2)*.

Characters (2) and (3) are the common conditions among colubrids (see, e.g., Klauber, 1943; Guyer and Donnelly, 1990; Shine, 1991).

(4) *Postorbital and frontal widely separated by a flange of the parietal (Fig. 38)*. This is the most common condition observed in a taxonomically and geographically diverse sample of terrestrial colubrids and, with the exception of *Pseudoxyrhopus* and *Liophidium*, the state in all Malagasy colubrids examined. It is therefore probably a plesiomorphic state for the *stumpffi* group.

(5) *Anterior end of the sphenoid broad and bifurcate (Fig. 39)*.

(6) *Lateral margins of the cultriform process of the sphenoid parallel or slightly diverging (Fig. 39)*. States (5) and (6) are uniformly present in species of the *stumpffi* group. The sphenoid, including the form of the cultriform process and of its anterior end, varies greatly in shape among colubrids. Both states are present in a taxonomically and geographically diverse array of colubrids, but both were uncommon states among the Malagasy colubrids examined (state (6) is seen in *Mimophis* and *Dromicodryas*). Given their universal presence in species of the *stumpffi* group, they probably are plesiomorphic within the group, but whether or not they are synapomorphies for the group remains unclear.

(7) *Ventral surface of sphenoid anterior to the anterior Vidian foramina flat or convex (no median groove or parallel bony ridges extending forward along the cultriform process from median protuberance)*. See discussion under *sexlineatus* group.

(8) *Ventral and posteroventral edges of frontal emarginate, resting high above the margins of the trabecular grooves on a high frontal crest of the sphenoid (Fig. 40)*. A consistent feature of species of the *stumpffi* group, the posteroventral margin of the frontal forms an angle  $>30^\circ$  with the dorsal margin of the trabecular grooves (cf. *sexlineatus* group). *Liopholidophis la-*

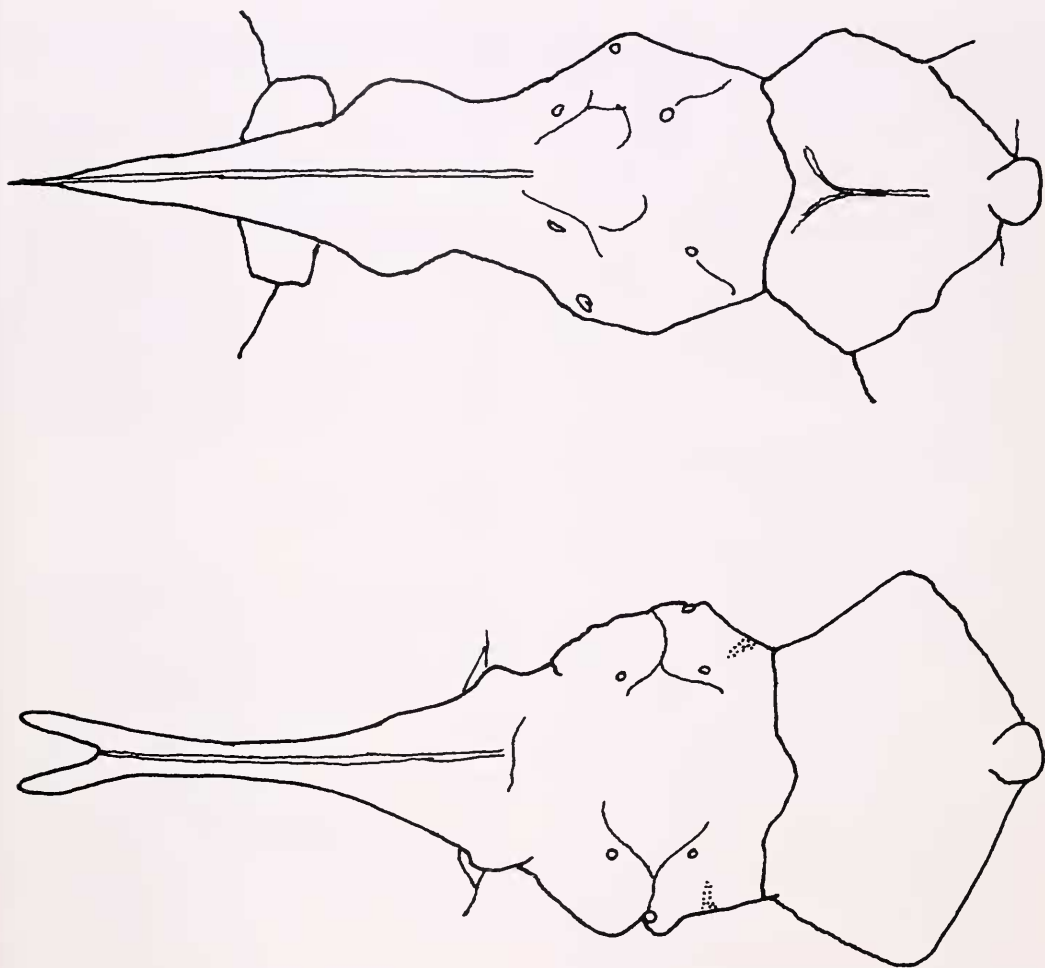


Figure 39. Basicranial region (sphenoid + basioccipital) of *Liopholidophis* showing differences between the *sexlineatus* and *stumpffi* groups (represented by *dolicocercus* and *lateralis*, respectively). Top: *L. doliocercus* (MCZ 180409). Bottom: *L. lateralis* (MCZ 180350). See text for discussion.

*teralis* seems to have the least emargination, whereas *epistibes* and *infrassignatus* are more emarginate. This character is widespread taxonomically and geographically within colubrids.

(9) *Dorsal plate of frontals, viewed as a unit, longer than the width at its narrowest point* (Fig. 38). See discussion under *sexlineatus* group.

(10) *No dark stripe on dorsal scale row 1* (cf. *sexlineatus* group).

(11) *Dorsolateral light stripe*. The light stripe is present on rows 5–7 or 5–6 in

*epistibes* and *infrassignatus*, rows 4–5 in *stumpffi*, and rows 3–5 in *lateralis*. A light stripe is present also in *rhadinaea* of the *sexlineatus* group (row 6 anteriorly, 5 posteriorly) but is otherwise absent in that group.

(12) *Apical pits present*. The number of apical pits appears to be highly variable even within a specimen (0–2 pits present) in the *stumpffi* group. The pits are readily detectable in some specimens; in others, a careful search is required to detect scattered scales with pits. When only a single

pit is present, it is asymmetrically placed to one side of the scale tip. Apical pits appear to be more consistently present and evident in *lateralis* (generally 2 pits) than in other members of the *stumpffi* group.

Scale pits in colubrids vary greatly in their obviousness (see, e.g., Conant, 1961); with the exception of *lateralis* (when they are present in that species), those in the *stumpffi* group are not as easily seen as those of many other colubrids. Nevertheless, all species of the *stumpffi* group have apical pits (none detected in the *sexlineatus* group).

(13, D) *Presence of dorsoventral neck flattening as a defensive display.* Three species of the *stumpffi* group flatten the neck as a defensive display (no observations for *stumpffi*). In at least *lateralis*, the display can involve a greater portion of the body. In all three species, the behavior highlights the white edges of the dorsal scales and exposes white skin between the scales. This behavior was not observed in any species of the *sexlineatus* group. The extent of white skin between the scales appears to vary within and among species. Often only small patches adjacent to white scale borders are white; in other cases, more extensive patches of skin are involved.

Neck flattening is found in diverse colubrids but seems to be rather taxonomically restricted (Greene, 1988). Myers (1986) used the behavior as a synapomorphy for a Neotropical clade (Xenodontini) comprising six genera. I have not observed the behavior in Malagasy colubrids outside members of the *stumpffi* group and, thus, consider it also as a synapomorphy of the group.

In addition to the use of neck flattening as a defensive display, *epistibes*, *lateralis*, and *infrassignatus* also bite readily in defense. This contrasts with species of the *sexlineatus* group, which appear to seldom bite in defense (see species accounts).

(14, D) *Distal tip of hemipenial lobes umbelliform (see hemipenial descriptions and discussion; Figs. 34–36).* Based on its apparently nearly unique occurrence in

species of the *stumpffi* group, this character is considered a synapomorphy for the group.

(15) *Undivided portion of hemipenis (stalk) reduced.* The stalk is especially reduced in *epistibes* and *stumpffi*, which essentially have none.

(16, D) *Expanded spinose midsection of hemipenis distinctly set off from narrower proximal portion of stalk by a nude shelf and/or delimiting groove.* Because of the unusual and apparently taxonomically restricted nature of this feature, the differentiated midsection of hemipenes in the *stumpffi* group is considered a synapomorphy.

#### Relationships within the Species Groups

Accepting the monophyly of each of the species groups of *Liopholidophis*, I here briefly explore hypothesized relationships within each group. These hypothesized relationships and supporting evidence are summarized in Figure 41.

***Sexlineatus* Group.** The following is a suggested synapomorphy scheme for species of the *sexlineatus* group and assumes the following plesiomorphic conditions for the group (characters invariant within the group not listed; see "Monophyly of the Species Groups of *Liopholidophis*").

(1) Minimal sexual dimorphism in relative tail length (<10% differences between means for the sexes; cf. Fig. 37). In having the least dimorphic tail length proportions, and in lacking other clearly derived character states, *pinguis* is considered the most plesiomorphic member of the *sexlineatus* group.

(2) Presence of vivid white borders on dorsal scale rows (present in *pinguis*, *sexlineatus*, and *grandidieri* in the *sexlineatus* group). Minimally involving dorsal row 3, but often other rows as well (see species accounts). Plesiomorphic condition inferred on the basis of presence of this character state in the *stumpffi* group (*stumpffi*, *epistibes*, *lateralis*, and *infrassignatus*).

(3) Ventrolateral black stripe on dorsal

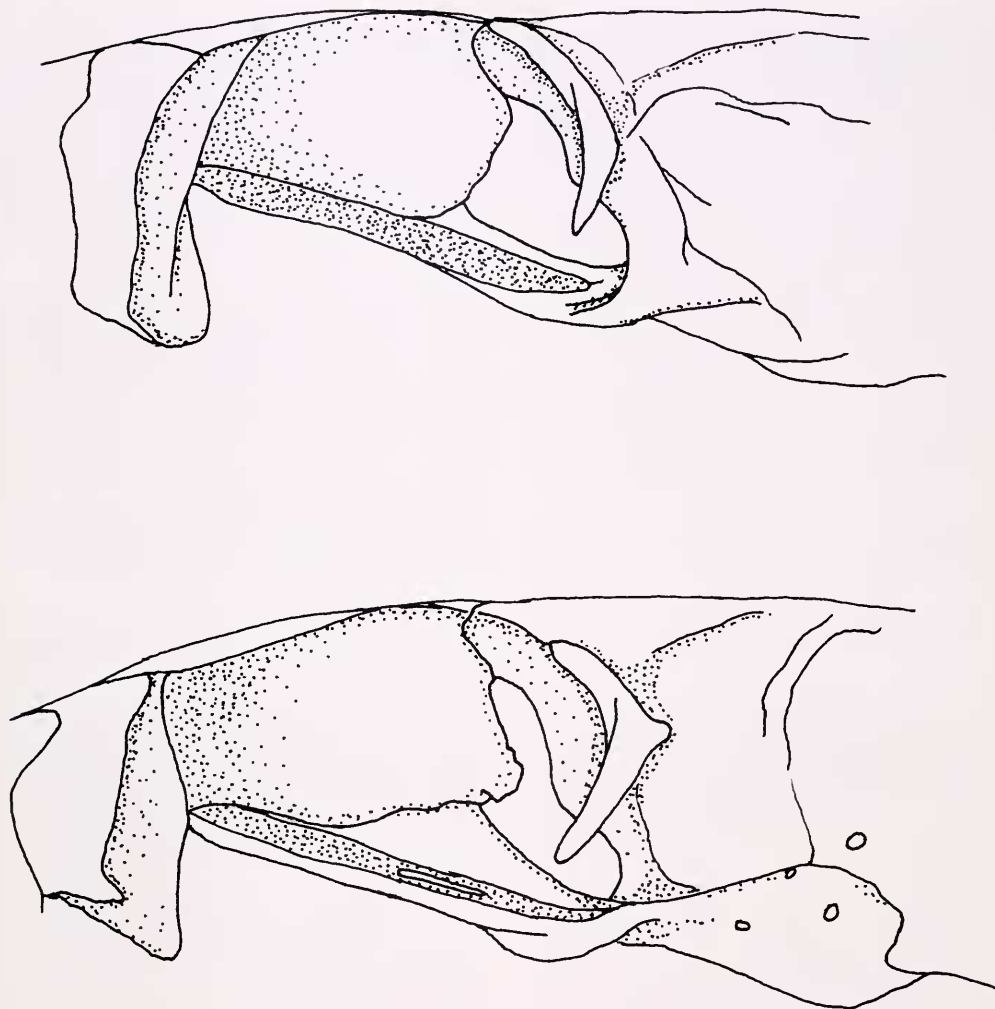


Figure 40. Orbital region of skulls of *Liopholidophis* showing differences between the *sexlineatus* and *stumpffi* groups (represented by *dolicercus* and *lateralis*, respectively). Top: *L. doliocercus* (MCZ 180409). Bottom: *L. lateralis* (MCZ 180350). See text for discussion.

row 1 or suture line between ventrals and row 1: well developed posteriorly (weak or absent anteriorly). In all species except *pinguis*, the stripe is well developed anteriorly as well.

(4) Lateral black stripe involving dorsal row 3 (may involve adjacent rows as well): well developed posteriorly. In *pinguis*, the stripe may be well developed (Parker, 1925) or weak (personal observations) anteriorly.

(5) Middorsal pattern uniform the length of the body. The median dorsal scale rows are uniform in ground coloration (i.e., not involving discrete mottling or blotching). Plesiomorphic condition inferred from the condition in the *stumpffi* group.

The diversity of hemipenial structure among species of the *sexlineatus* group and questionable outgroup structure made use of hemipenial characters for comparative purposes here virtually impossible.

The following characters unite clades within the *sexlineatus* group (**D** = derived; cf. Fig. 41; for ease of interpreting Fig. 41, and for distinguishing them from characters in the previous section, these characters are given letter designations):

(*dolicocercus, grandidieri*): (a, **D**) dorsal pattern consisting of complex mottling or reticulations of black and brown anteriorly, black chevrons or blotches posteriorly; (b, **D**) ventral pattern of complete and uniform blackening of ventral scutes (except laterally in *dolicocercus*). Both patterns, but especially the ventral one, are unusual not only in *Liopholidophis*, but among colubrids generally; (c) lateral black stripe anteriorly involving scale rows 3–4 (vestigial anteriorly, and completely absent posteriorly in *dolicocercus*) (In *sexlineatus* and *pinguis*, rows 2–3 are involved, and the stripe is absent in *rhadinæa*).

(*rhadinæa (dolicocercus, grandidieri)*): (d, **D**) Loss of vivid white borders to dorsal scale rows. Plesiomorphic condition of presence of white borders, as already inferred. Postulating loss of white borders as a synapomorphy of this clade requires reacquisition in *grandidieri* (i.e., loss then gain). However, based on the distribution of other postulated derived states (Fig. 41) two independent losses would otherwise be required (in *rhadinæa* and *dolicocercus*).

(*sexlineatus (rhadinæa (dolicocercus, grandidieri))*): (e, **D**) Development of extreme sexual dimorphism in relative tail length (>10% difference between means of relative tail lengths for males and females; see Fig. 37). *Liopholidophis pinguis*, in having the least dimorphic tail proportions, is thereby considered the most plesiomorphic species of the *sexlineatus* group. Nonetheless, the phylogeny hypothesized in Figure 41 suggests that sexual dimorphism in tail length has not progressively increased during the evolution of the *sexlineatus* group: *sexlineatus* and *grandidieri*, the two species with greatest male tail lengths and greatest dimorphism in relative tail length (Fig. 37), are not sister taxa. If the degree of tail dimorphism

has had a complex evolutionary history, then hypothesizing that *pinguis* is the sister species to the rest of the *sexlineatus* group on the basis of having the least tail dimorphism may be overly simplistic. However, based on characters examined, *pinguis* seems to share no unequivocally derived features with other species in the group.

**Stumpffi Group.** I have been less successful postulating relationships among species of the *stumpffi* group. In part this is due to these snakes seemingly being more generalized than those of the *sexlineatus* group, and in part to the mosaic distribution of character states among them (Table 3). Given the questionable monophyly of *Liopholidophis* and lack of explicit outgroups, I have been unable to unambiguously polarize the variable characters (Table 3).

*Liopholidophis stumpffi* and *epistibes* are superficially more similar to one another (longer tails with more subcaudals, more gracile habitus than *lateralis* and *infrassignatus*) and have an extremely bilobed hemipenis (essentially no basal stalk), which seems to be a more derived morphology than the less bilobed organs of the other two species (f, **D**). Hence, I postulate that *stumpffi* and *epistibes* are sister species on this basis (Fig. 41), but any hypothesis of relationships within this group seems poorly supported with present information.

#### NOTES ON MNHN 1988-331 (GENUS AND SPECIES INQUIRENDA)

##### Figure 42

In several instances I alluded to problems concerning the generic limits of both *Liopholidophis* and *Liophidium* (see Discussion under the description of *rhadinæa*; "Monophyly of *Liopholidophis*"). The problem is sharply focused by one specimen with a mosaic of characteristics of both genera. Domergue (1988:143, "Specimen 1") referred MNHN 1988-331 to *Liophidium incertae sedis*, but the specimen is similar to *Liopholidophis rhadi-*

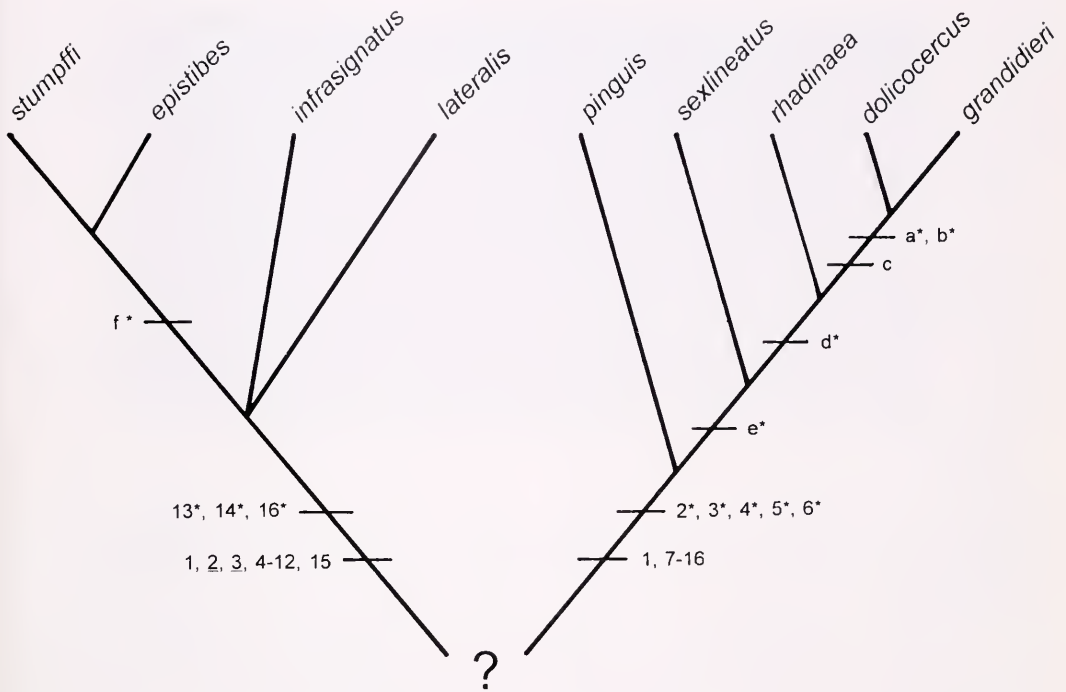


Figure 41. Hypothesized phylogenetic relationships and character summary for species of *Liopholidophis*. As noted in the text, the monophyly of *Liopholidophis sensu lato* is equivocal. Numbered characters discussed in the section "Monophyly of the Species Groups of *Liopholidophis*"; lettered characters discussed under "Relationships within the Species Groups." Asterisked (\*) characters are putative derived characters; underlined characters have plesiomorphic states at the levels indicated; characters with neither designation cannot be postulated as either derived or primitive at the level indicated. The numbered characters, which define the two species groups, have alternative states for each group (see text).

*naea* in overall appearance, although more gracile and with a less distinct head. Comparison of its everted hemipenes with those of *rhadinaea* reveal that the organs are nearly identical! Nevertheless, other characteristics make this specimen particularly enigmatic. (Domergue's [1988] *Liophidium* "Specimen 2" is a *Liopholidophis rhadinaea*, which is superficially similar to some species of *Liophidium*.) Hence, I amplify Domergue's treatment of MNHN 1988-331 in order to put the problem of generic limits in a broader perspective.

MNHN 1988-331 (Fig. 42) was collected 10 December 1966 at Perinet [=Andasibe] according to a tag attached to the specimen (Domergue [1988] gave the collection date as 19 December 1966 and the collector as E. R. Brygoo). It is a male,

apparently adult, as indicated by mineralized spines on the hemipenes (Domergue [1988] reported the specimen as a juvenile), with hemipenes everted. Total length 313 mm, tail length 92 mm (29% of total), head barely wider than neck; 15-15-15 smooth dorsal scale rows without apical pits; 149 ventrals, divided anal plate, 77 subcaudals; loreal present, 1-1 preoculars, 2-2 postoculars, 1-1 anterior temporals, 1-1 posterior temporals; 8-8 supralabials (4-5 touching eye) and 9-9 infralabials. The specimen has 27 + 2 right maxillary teeth, the fangs ungrooved and about twice the size of the teeth immediately preceding (Domergue states "25-30 maxillary teeth"). Teeth curved, sharp, of normal proportions, and firmly ankylosed to the bone. The articulation between the dentary and

TABLE 3. VARIATION IN QUALITATIVE CHARACTERISTICS AMONG SPECIES OF THE *LIOPHOLIDOPHIS STUMPFII* GROUP.

	<i>stumpffi</i>	<i>epistibes</i>	<i>lateralis</i>	<i>infrassignatus</i>
Relatively long tail (high subcaudal counts)	yes	yes	yes (males)	no
Dorsolateral stripe	rows 4-5	rows 5-6 or 5-7 (4-5 posteriorly)	rows 3-4-5 (occasionally 4 only)	rows 5-6
Light stripe confluent with light throat	yes	no	yes	no
Stripe complete the length of body and tail	Body: sometimes Tail: sometimes	Body: sometimes Tail: sometimes	Body: yes Tail: yes	Body: rarely Tail: no
Venter <sup>1</sup>	more or less immaculate	usually heavily pigmented	immaculate	usually heavily pigmented
Ventral counts relatively low (mean <ca. 150)	yes	no (>160 both sexes)	no (155, males; 160, females)	yes
Maxillary teeth (mean)	>25	>25	>25	<25
Enlarged spines encircling base of hemipenial lobes	single row; few	multiple rows; many	sparse, spines clustered; few	multiple rows; many
Hemipenial stalk	very short	very short	long	intermediate
Sulcus spermaticus <sup>2</sup>	forked $\geq 75\%$ its length	forked $\geq 75\%$ its length	forked ca. 60% its length	forked ca. 70% its length

<sup>1</sup> All species of the *stumpffi* group may have encroachment of dorsal pigment and/or dark dots at lateral edges of ventrals. This comparison refers to additional ventral pigmentation.

<sup>2</sup> The length of the basal unforked portion of the sulcus spermaticus is correlated with the length of the hemipenial stalk, so these two characters may not be independent. However, nothing would seem to preclude a snake having a long hemipenial stalk from having the sulcus divide basally and, thus, having a short unforked portion of the sulcus.

the compound bone of the lower jaw appears to be about half way along the length of the dentary. The presence of hypapophyses on posterior trunk vertebrae was not verified.

*Coloration in Life (Domergue, 1988: 144, Paraphrased).* "Dorsum reddish brown; the head equally reddish brown (but darker than the body) and having three light yellow spots; the upper labials white, spotted with brown; venter red except for the throat, which is white."

*Coloration and Pattern in Preservative.* General dorsal coloration medium brown to yellowish brown. Dorsolateral light stripe on lower portion of dorsal row 5, bordered above and below by a slightly darkened series of dashes; the light stripe continuous from neck to near the end of the tail and tending to be a series of dashes on the tail. Rows 1-3 light brown; the 3 middorsal

rows slightly darker brown than adjacent 1½ rows, which border the dorsolateral light stripe. Three small light nape spots, each surrounded by a dark brown line. Top of head brown; head cap separated from white supralabials by a thin dark brown streak along dorsal border of supralabials. A few scattered brown spots on posterior supralabials. Venter and subcaudals, including throat, gular region, and infralabials, immaculate whitish. No dark pigment at edges of ventrals, or on scale row 1 except posteriorly, where a series of small brown spots is present; the latter continues onto the tail to become a continuous line at the lateral edges of the subcaudals.

*Hemipenis.* Both hemipenes of MNHN 1988-331 were everted upon preservation, the left one completely, the right organ with the tips of the lobes remaining inverted. The left organ has a total length



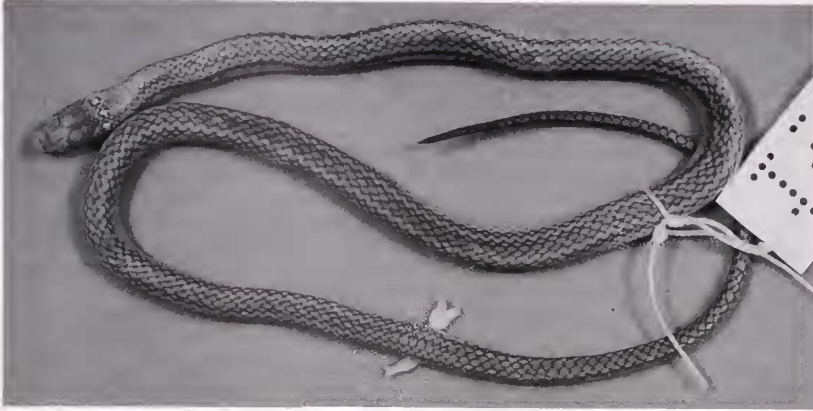


Figure 42. MNHN 1988-331, genus and species *inquirenda*. Approximately  $\times 1.2$ .

of approximately 5 mm, the length of the lobes approximately 2 mm. The sulcus spermaticus divides about 2.5 mm from the base of the organ. The organ is deeply bilobed, noncapitate, acalyculate (entirely spinose), with small nude areas at the tips of the lobes, and a deeply bifurcate centrolineal sulcus spermaticus. No basal pockets or lobes.

The sulcus spermaticus is a deep groove, bifurcate for half its length, the branches terminating on the same side of the organ at the tips of the lobes (centrolineal in orientation). The tips of the branches of the sulcus on the left organ are difficult to discern, as if they simply peter out rather than having a discrete endpoint (distal tips narrow and very shallow; proper lighting necessary to see the ends).

The stalk (about 40% the length of the organ) is covered on all sides with small hooked spines. The stalk abruptly broadens below the sulcus division, the spines coincidentally increasing in size (spines here about twice as large as those on the base of the stalk). The lobes, including the crotch and inner and outer surfaces, are covered with hooked spines except for the distal nude tips of the lobes. The spines are arrayed more or less in longitudinal rows.

The tips of the lobes are nude but not appearing as cylindrical or as discrete as the awns on the hemipenis of *Liopholidophis rhadinaea*.

*Discussion.* Domergue (1988) did not give reasons for referring MNHN 1988-331 to *Liophidium*. Other than head proportions (head small and little distinct from neck), the specimen shares few features with other species of *Liophidium*. The dentition (sharp, curved teeth; enlarged rear maxillary teeth) and a "normal" articulation between the dentary and compound bone of the lower jaw (see Discussion under *Liopholidophis rhadinaea*) seem to preclude association of MNHN 1988-331 with *Liophidium* as usually defined (Boulenger, 1896; cf. also Savitzky, 1983; rear maxillary teeth in some *Liophidium* are somewhat enlarged, but not to the extent seen in MNHN 1988-331 in specimens I examined). Other features, such as the lack of scale row reductions, 15 dorsal rows, labial formulae, and relative tail length, are variable among the nominal taxa presently in *Liophidium* (approximately 8 species in Madagascar and the Comoro Islands; Domergue, 1983, and personal observations). An unusual feature of MNHN 1988-331 appears to be the presence of a single posterior temporal (2 in other species of *Liophidium*; Guibé, 1958, and personal observations).

The most puzzling aspects of MNHN 1988-331 are the striking similarities to *Liopholidophis rhadinaea* in color pattern, dentition, and hemipenis, but notable differences in most other aspects of scalation

and body proportions. These similarities include (1) darkened middorsal 3 scale rows, although not so darkened in MNHN 1988-331 as in *rhadinæa*; (2) dorsolateral light brown stripe (row 5 in MNHN 1988-331 vs. centered on row 6 in *rhadinæa*); (3) three light nape spots surrounded by narrow dark brown line (smaller in MNHN 1988-331 than in *rhadinæa*); (4) top of head plain brown and unpatterned; (5) dark brown line at upper edge of supralabials separating head cap from white supralabials (line not so dark or broad in MNHN 1988-331 as in *rhadinæa*); (6) immaculate venter, red in life *vide* Domergue (1988) (pink to vermilion in *rhadinæa*); (7) dentition similar in overall appearance, and maxillary tooth number for MNHN 1988-331 within the range of variation seen in *rhadinæa*; and (8) overall similarity in hemipenial morphology.

The hemipenes of *Liopholidophis rhadinæa* and MNHN 1988-331 are similar in form, differing mainly in two features: (1) the cylindrical awns at the tips of the lobes in *rhadinæa* are discrete structures, somewhat set off from the body of the lobes (Fig. 30), whereas the nude tips of the lobes in MNHN 1988-331 are not so discretely set off; and (2) the sulcus spermaticus in *rhadinæa* terminates at the base of the awns with a discrete endpoint, whereas the branches of the sulcus in MNHN 1988-331 appear to extend to the tips of the lobes, where they peter out rather than having a discrete endpoint. The organ of *rhadinæa* may have a somewhat more dense array of spines on the lobes than MNHN 1988-331, but the difference is subtle. Although the hemipenis of MNHN 1988-331 differs in these ways from that of *rhadinæa*, the organs of the two are exceedingly similar for snakes that otherwise differ in many ways (more similar, for example, than the hemipenis of *rhadinæa* is to any other species of *Liopholidophis*).

In addition to having unreduced 15 dorsal scale rows, scale counts and tail proportions of MNHN 1988-331 are well outside the ranges for males of *Liopholidophis rhadinæa* (cf. Table 1): ventrals 149 (vs.

170-179), subcaudals 77 (vs. 126-137), and tail relative to total length 29% (vs. 37-43%).

Its peculiar mosaic suite of characteristics do not allow unambiguous allocation of MNHN 1988-331 to any Malagasy colubrid genus as currently defined. That, along with questions already raised concerning the proper definition of *Liopholidium vis-à-vis* similarities between *Liopholidophis rhadinæa* and *Liopholidium*, differences among species of *Liopholidium* (see Discussion after description of *L. rhadinæa*), and the questionable monophyly of *Liopholidophis*, suggest that future work may result in reallocation of some nominal taxa with improved understanding of phylogenetic relationships among Malagasy colubrids. The question with respect to *Liopholidium* is the extent of interspecific variation in the "unique" dentitional and other skull characteristics attributed to that genus (Boulenger, 1896: 598-599; Savitzky, 1981, 1983), particularly in the new species recently described (Domergue, 1983). Such investigation remains to be done.

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of the holotype of *Liopholidophis doliocercus*, provided information on its provenience, and clarified some locality information. Laszlo Meszoly prepared the illustrations of hemipenes. Alan Savitzky shared his knowledge of *Liophidium* and discussed skull morphology of *Liopholidophis* with me; Chuck Myers advised me on some aspects of hemipenial morphology. For loan of specimens I am grateful to R. F. Inger and H. Voris (FMNH); C. W. Myers and L. Ford (AMNH); K. Klemmer and M. Landau (SMF); and R. W. McDiarmid, R. P. Reynolds, and G. R. Zug (USNM). Special thanks to the staffs of The Natural History Museum, London (E. N. Arnold, C. McCarthy, and B. Clarke) and the Museum National d'Histoire Naturelle, Paris (I. Ineich and A. Dubois) for cordial hospitality and assistance during my visits to their institutions. Chris Raxworthy facilitated my examination of the type of *grandidieri*. Charles W. Myers and Harry W. Greene commented on the manuscript. For their thorough and generous support I am grateful to M. Benjamin Andriamihaja, Mme. Berthe Rakotosamimanana (MINISUP), Mme. Celestine Ravaoarimomanga (MPAEF), M. Philemon Randrianarijaona (Directeur des Eaux et Forêts), and countless other Malagasy friends. Finally, but critically, a grant from the Ernst Mayr fund of the MCZ permitted examination of types and other material at the BMNH and the MNHN; it is a tribute to a scientist of Mayr's stature that, realizing the continued critical need for support of museum-based systematic work for understanding life on earth, he established the Mayr fund to support this most basic biological enterprise. Publication costs were covered, in part, by the Wetmore-Colles Fund.

#### APPENDIX: SPECIMENS EXAMINED

The following abbreviations of collections are used in the text and in the list of specimens examined. As all specimens are from Madagascar, localities begin with the province. Coordinates are given for those localities that could be reliably localized.

However, because Malagasy place names are highly redundant, coordinates were not readily apparent for some older specimens examined for which no provinces were given. Bracketed information in localities are inferred political units (province and, where possible, fivondronana), coordinates, or updated names for towns. Parenthetical expressions within localities are part of the original locality data. A useful reference for names of smaller political units within provinces (fivondronanas) is Brygoo (1971:map 4, p. 36), although some must now be updated to reflect current name usage. Some localities are annotated with collector or other historical information that help localize older sites. Skeletal preparations examined are indicated as *sk* (skull) or *skel* (complete skeleton, including skull). Specimens of *rhadinaea* and *epistibes* are listed in the descriptions of those species.

AMNH	American Museum of Natural History, reptile collection, New York
BMNH	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, reptile collection, Harvard University, Cambridge
MNHN	Museum National d'Histoire Naturelle, Paris
MZUT	Museo Zoologica dell'Università di Torino [now incorporated as part of the Museo Regionale di Scienze Naturali di Torino], Torino
SMF	Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

#### *Liopholidophis doliocercus* (Peracca)

**FIANARANTSOA:** *Fivondronana Ifanadiana*: Talatakely, Ranomafana National Park, 970–1,050 m [21°16'S, 47°25'E], MCZ

180403-08. Mountain ridge N Miaranony, approximately 9.8 km WNW (airline) Tsaratanana, Faravory River, Ranomafana National Park, 800 m [21°09'30"S, 47°33'E], MCZ 180409 (*skel*). [**TOAMASINA: Fivondronana Moramanga**]: "Valle dell'Umbi (Andrangoloka)" [Valley of the Umbi River (Andrangoloka)] [=Andrangoloaka] [19°02'S, 47°55'E], MZUT 0796 (holotype; color slides only seen). Moramanga, eastern Madagascar [18°56'S, 48°12'E], SMF 17575 (=7246.1a, as listed by Boettger, 1898:25, 1913:312).

*Liopholidophis grandidieri*  
Mocquard

[**FIANARANTSOA: Fivondronana Ambositra**]: Ambohitombo Forest, Madagascar [20°43'S, 47°26'E], BMNH 95.7.4.32 (specimen b of Boulenger, 1896:607 [as *Tropidonotus doliocercus*]). *Fivondronana Ifanadiana*: Mt. Maharira, Ranomafana National Park, approximately 1,375 m [21°19'59"S, 47°24'57"E], MCZ 180297 (*sk*). [**? TOAMASINA**]: Eastern Imerina, BMNH 95.10.29.52 (specimen a of Boulenger, 1893:247 [as *Tropidonotus doliocercus*]; see remarks under "Distribution" in species account for this locality). [**TOLIARA: Fivondronana Toliara**]: L'embouchure du Saint-Augustin ["mouth of the Saint-Augustin River," here considered to be in error] [23°33'S, 43°46'E], MNHN 02-103 (holotype) [the Saint-Augustin River is now referred to as the Onilahy River, and the town of Saint-Augustin at its mouth as Ianantsony or Anantsony].

*Liopholidophis infrasignatus*  
(Günther)

**NO SPECIFIC LOCALITIES**: "Imerina," BMNH 95.10.29.53-55 (specimens k-m of Boulenger [1893:248], as [*Liopholidophis*] *stumpffii*; see remarks under "Distribution" in *grandidieri* species account for this locality). [**FIANARANTSOA: Fivondronana Ambohimahaso**]: Arkafana, eastern Betsileo [=Ankafana *fide* Boulenger,

1893:247; 21°12'S, 47°12'E; 1,600 m *fide* Carleton and Schmidt, 1990; see "Remarks" in account for *infrasignatus*], BMNH 1946.1.7.57 (lectotype, herein designated); BMNH 1946.1.7.56, 1946.1.7.58 (paralectotypes). [**Fivondronana Ambositra**]: Ivohimanita [approximately 20°50'S, 47°30'E], BMNH 96.10.9.16-17 [specimens collected by Major, who, discussing the locality as "Ivohimanitra" (Major, 1896), gave the elevation as 1,000-1,100 m; MacPhee (1987) gives 700 m, whereas Carleton and Schmidt (1990) give 900 m]. *Fivondronana Ifanadiana*: Talatakely, Ranomafana National Park, 970 m [21°16'S, 47°25'E], MCZ 180354-70 (180357, *skel*; 180370, *sk*). Ivalohoaka, Ranomafana National Park, approximately 1,040 m [21°17'50"S, 47°26'20"E], MCZ 180371. Mountain ridge N Miaranony, approximately 9.8 km WNW (airline) Tsaratanana, Faravory River, Ranomafana National Park, 850 m [21°09'30"S, 47°33'E], MCZ 180373. Approximately 2.2 km (airline) SE Sahavondrona along Andranoroa River, 1,170 m [21°17'10"S, 47°21'20"E], MCZ 180372. *Fivondronana Midongy du Sud*: Approximately 7 km SW (airline) Midongy du Sud [=Midongy Atsimo], near Rianambo ("high waterfall") on Alapo River, 670 m [23°35'S, 47°01'E], MCZ 180374. [**TOAMASINA: Fivondronana Moramanga**]: Moramanga [18°56'S, 48°12'E], SMF 17578. Perinet forestry station, 900 m [=Andasibe; 18°56'S, 48°25'E], MNHN 1971-332 (holotype of *Liopholidophis thieli* Domergue). 8 km E Perinet [=Andasibe; 18°56'S, 48°25'E], USNM 149895.

*Liopholidophis lateralis*  
(Duméril, Bibron, and Duméril)

**NO SPECIFIC LOCALITIES**: "Madagascar," BMNH 71.6.28.17, 1946.1.15.19 (syntypes of *Dromicus madagascariensis* Günther). [**ANTANANARIVO: Fivondronana Manjakatampo**]: Monjakatampo [=Manjakatampo], 10 km W Ambatolompy [=Ambatolampy] [19°20'S, 47°26'E; 1940 m *fide* Angel, 1934], AMNH 60675-76, 60679-80 (60676, *sk*). **FIANARANTSOA**:

[*Fivondronana Fianarantsoa*]: Fianarantsoa [21°26'S, 47°05'E], SMF 57037. *Fivondronana Ifanadiana*: 1–2 km W Ranomafana (by trail on S side of Namorona River), approximately 700 m [21°15'S, 47°27'E], MCZ 180344–45. Trail between Tsaratanana and Ambohipo, approximately 400–500 m [21°11'S, 47°37'E], MCZ 180346–52 (180350, *skel*). Talatakely, Ranomafana National Park, 970 m [21°16'S, 47°25'E], MCZ 180353. *Fivondronana Midongy du Sud*: Approximately 4 km SW (airline) Midongy du Sud [=Midongy Atsimo], approximately 600 m [23°35'S, 47°01'E], MCZ 180380. Approximately 7 km SW (airline) Midongy du Sud [=Midongy Atsimo], near Rianambo (“high waterfall”) on Alapo River, 670 m [23°35'S, 47°01'E], MCZ 180375. [**MAHAJANGA**: *Fivondronana Mahajanga*]: Majunga [=Mahajanga; 15°43'S, 46°19'E], SMF 17586, 57163. [**TOAMASINA**: *Fivondronana Toamasina*]: Tampina [18°30'S, 49°16'E; part of Bluntschili collection; see Mertens, 1933], AMNH 71498. 85 km N Mormunga [<sup>?</sup> = Moramanga; ?18°56'S, 48°12'E], USNM 149243. [**TOLIARA**: *Fivondronana Tolagnaro*]: Eminiminy [approximately 24°40'S, 46°55'E], AMNH 71506 [part of Bluntschili collection; in the Ambolo (=Manampanihy) Valley and 400 m elevation *fide* Mertens, 1933:261]. *Fivondronana Betroka*: Betroka [23°16'S, 46°05'E], USNM 149374–75. [<sup>?</sup> *Fivondronana Moramanga*]: “Eastern forest” [about half way between Tamatave (=Toamasina) and Tananarive (=Antananarivo)], MCZ 11659–68, 11670–73, 11675–81 (see “Remarks” in *pinguis* species account for discussion of locality).

*Liopholidophis pinguis*  
Parker

**NO SPECIFIC LOCALITIES**: “Nord-Madagascar,” SMF 61909. “Madagascar,” AMNH 60692. [**TOAMASINA**: *Fivondronana Ambatondrazaka*]: Lake Alaotra [17°30'S, 48°30'E], BMNH 1936.3.3.94–97. [*Fivondronana Moramanga*]: Perinet [=Andasibe; 18°56'S, 48°25'E], USNM

149242. [<sup>?</sup> *Fivondronana Moramanga*]: “Eastern forest” [about half way between Tamatave and Tananarive], MCZ 11698–11701 (11701, *sk*) (see “Remarks” in *pinguis* species account for discussion of locality).

*Liopholidophis sexlineatus*  
(Günther)

**NO SPECIFIC LOCALITIES**: “Eastern Betsileo,” BMNH 1946.1.13.17–19 (old numbers 82.5.8.2–4) (syntypes of *Dromicus sexlineatus* Günther); BMNH 1946.1.13.28–30 (old number 82.2.25) (syntypes of *Dromicus macrocerus* Günther). See “Remarks” in species account for locality comments. **INDETERMINATE LOCALITY**: Mangerano, SMF 57028, collected by K. L. Koch (probably = Mangarano; the Defense Mapping Agency [1989] lists 12 localities with this name; the SMF has specimens collected by Koch from widely scattered localities in Madagascar, so the particular locality represented by SMF 57028 is unclear). **ANTANANARIVO**: *Fivondronana Manjakatompoto*: Monjakatompoto [=Manjakatompoto], 10 km W Ambatolompy [=Ambatolampy] [19°20'S, 47°26'E; 1940 m *fide* Angel, 1934], AMNH 60678 (*sk*). **FIANARANTSOA**: *Fivondronana Ifanadiana*: Ambatolahy, approximately 2.3 km NW (airline) Ranomafana, approximately 850 m [21°14'55"S, 47°25'48"E], MCZ 180325–35 (180332, *skel*). Approximately 2.2 km (airline) SE Sahavondrona along Andranoroa River, 1,170 m [21°17'10"S, 47°21'20"E], MCZ 180336–37. Ambodirafia [21°19'S, 47°35'E], MCZ 180338. *Fivondronana Midongy du Sud*: Approximately 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo (“high waterfall”) on Alapo River, 670 m [23°35'S, 47°01'E], MCZ 180376–79. [**TOAMASINA**]: Eastern forest [about half way] between Tamatave (=Toamasina) and Tananarive (=Antananarivo)], MCZ 11602–06 (see comment on this locality in species account remarks for *L. pinguis*).

*Liopholidophis stumpffi*  
(Boettger)

[*ANTSIRANANA: Fivondronana Antsirananana*]: Route from Antsohihy NW to Diego Suarez, NE Madagascar [approximately 12°20'S, 49°05'E], MCZ 54368. Montagne d'Ambre [=Ambohitra; 12°30'S, 49°10'E], MNHN 1893.211 (syntype of *Liophidium gracile* Mocquard), USNM 150595. [*Fivondronana Nosy Be*]: Nossi-Bé [=Nosy Be; 13°20'S, 48°15'E], SMF 17576 (lectotype, herein designated), 17577, 17580-84; FMNH 18291; BMNH 1946.1.23.51; MNHN 84-595 (syntype of *Liophidium gracile* Mocquard).

## LITERATURE CITED

- AHL, E. 1928. Neue Frösche der Gattung *Rhacophorus* aus Madagaskar. *Zoologischer Anzeiger*, 75(11/12): 311-318.
- ANGEL, F. 1934. Sur une collection de reptiles et de batraciens de Madagascar. *Faune des Colonies Françaises* 5(6): 311-320.
- . 1936. Matériaux herpétologiques recueillis à Madagascar par M. Roger Heim, Chargé de Mission: description de deux formes nouvelles. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, ser. 2, 8: 125-129.
- ARNOLD, S. J. 1988. Quantitative genetics and selection in natural populations: microevolution of vertebral numbers in the garter snake *Thamnophis elegans*, pp. 619-636. In B. S. Weir, E. J. Eisen, M. J. Goodman, and G. Namkoong (eds.), *Proceedings of the Second International Conference on Quantitative Genetics*. Sunderland, Massachusetts: Sinauer Associates.
- ARNOLD, S. J., AND A. F. BENNETT. 1988. Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake (*Thamnophis radix*). *Biological Journal of the Linnean Society*, 34: 175-190.
- BARBOUR, T. 1918. Vertebrata from Madagascar. 2. Amphibia and Reptilia. *Bulletin of the Museum of Comparative Zoology*, 61: 479-489.
- BASTARD, E. J. 1898. Quelques mots sur une mission à Madagascar. *Bulletin du Muséum d'Histoire Naturelle*, Paris, 4: 248-251.
- BLACKBURN, D. G. 1993. Standardized criteria for the recognition of reproductive modes in squamate reptiles. *Herpetologica*, 49(1): 118-132.
- . 1994. Review: discrepant usage of the term 'ovoviviparity' in the herpetological literature. *Herpetological Journal*, 4: 65-72.
- BLOMMERS-SCHLÖSSER, R. M. A., AND C. P. BLANC. 1991. *Faune de Madagascar* 75 (1): Amphibiens (première partie). Paris: Muséum National d'Histoire Naturelle. 379 pp.
- BOETTGER, O. "1879" [1877]. Die Reptilien und Amphibien von Madagascar. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 11: 1-56.
- . 1881a. Diagnoses reptilium et batrachiorum novorum ab ill. Antonio Stumpff in insula Nossi-Be Madagascariensi lectorum. *Zoologischer Anzeiger*, 4(87): 358-362.
- . 1881b. Die Reptilien und Amphibien von Madagascar. Dritter Nachtrag. I. Studien über Reptilien und Amphibien von Madagascar. II. Aufzählung der bis jetzt von Madagascar und seinen Küsteninseln bekannt gewordenen Reptilien und Amphibien. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 12: 435-558.
- . 1898. *Katalog der Reptilien-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main*. II (Schlangen). Frankfurt am Main: Druck von Gebrüder Knauer. 160 pp.
- . 1913. Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas (Sammlung Voeltzkow 1889-1895 und 1903-1905), pp. 269-375 [+pls. 23-30]. In A. Voeltzkow (ed.), *Reise in Ostafrika in den Jahren 1903-1905 (Wissenschaftliche Ergebnisse, Band III. Systematische Arbeiten, Heft IV)*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, Nägele & Dr. Sproesser.
- BOULENGER, G. A. 1888. Descriptions of new reptiles and batrachians from Madagascar. *Annals and Magazine of Natural History*, 1, ser. 6: 101-107.
- . 1893. *Catalogue of the Snakes in the British Museum (Natural History)*, Vol. I. London: British Museum (Natural History). 448 pp.
- . 1896. *Catalogue of the Snakes in the British Museum (Natural History)*, Vol. III. London: British Museum (Natural History). 727 pp.
- . 1915. A list of snakes of Madagascar, Comoro, Mascarenes and Seychelles. *Proceedings of the Zoological Society of London*, 1915: 369-382.
- BRYGOO, E. R. 1971. Reptiles: Sauriens: Chamaeleonidae: genre *Chamaeleo*. *Faune de Madagascar*, 33: 1-318.
- . 1983. Les ophidiens de Madagascar. *Mémoires do Instituto Butantan*, 46(1982): 19-58.
- . 1987. L'Endémisme des reptiles de Madagascar. *Bulletin de la Société Zoologique de France*, 112: 5-38.
- CADLE, J. E. 1995. A new species of *Boophis* (Anura: Rhacophoridae) with unusual skin glands from Madagascar, and a discussion of variation and sexual dimorphism in *Boophis albilabris* (Boulenger). *Zoological Journal of the Linnean Society*, 115, in press.
- CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents

- (Muroidea: Nesomyinae): an annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987**: 1-36.
- CONANT, R. 1961. A new water snake from Mexico, with notes on anal plates and apical pits in *Natrix* and *Thamnophis*. American Museum Novitates, **2060**: 1-22.
- COWAN, W. D. 1883. Notes on the natural history of Madagascar. Proceedings of the Royal Physical Society of Edinburgh, **7**: 133-150.
- DEFENSE MAPPING AGENCY. 1989. Gazetteer of Madagascar, 2nd edition. Washington, D.C.: Defense Mapping Agency. xvii + 826 pp.
- DOMERGUE, C. A. 1962. Observations sur les pénis des Ophidiens (deuxième note). Bulletin de la Société des Sciences Naturelles et Physiques du Maroc, **42**(1-2): 87-105.
- . "1973" [1972]. Etude de trois serpents malgaches: *Liopholidophis lateralis* (D. & B.), *L. stumpfi* (Boettger) et *L. thieli* n. sp. Bulletin du Muséum National d'Histoire Naturelle, Paris, 3e ser., no. 103, Zool. **77**: 1397-1412.
- . 1983. Notes sur les serpents de la région malgache. III. Description de trois espèces nouvelles rapportées au genre *Liophidium* Boulenger, 1896. Bulletin du Muséum National d'Histoire Naturelle, Paris, ser. 4, **5**(sect. A, no. 4): 1109-1122.
- . 1988. Notes sur les Serpents de la région Malgache VIII. Colubridae nouveaux. Bulletin du Muséum National d'Histoire Naturelle, Paris, 4 ser., **10**(sect. A, no. 1): 135-146.
- DOWLING, H. G. 1959. Apical papillae on the hemipenes of two colubrid snakes. American Museum Novitates, **1948**: 1-7.
- DOWLING, H. G., AND J. M. SAVAGE. 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica, **45**: 17-31.
- DUMÉRIL, A. M. C., G. BIBRON, AND A. DUMÉRIL. 1854. *Erpétologie Générale*, Vol. 7. Paris: Muséum National d'Histoire Naturelle. Première Partie, vii + 4 + xvi + 780 pp; Deuxième Partie, xii + 780-1536 pp.
- ELTER, O. 1981. *Catologhi V.—La Collezione Erpetologica del Museo di Zoologia dell'Università di Torino*. Torino: Museo Regionale di Scienze Naturali, Torino. 116 pp.
- FISCHER, J. G. 1884. Über einige afrikanische Reptilien, Amphibien und Fische des Naturhistorischen Museums. II. Über einige Reptilien von Nossi-Bé und Madagaskar. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, **1**: 33-38.
- GALLIENI, J. S. 1908. Neuf ans à Madagascar. Paris: Librairie Hachette et Cie. xv + 372 pp.
- GLAW, F., AND M. VENCES. 1992. A Fieldguide to the Amphibians and Reptiles of Madagascar. Köln, Germany: Privately Published. 331 pp.
- . 1994. A Fieldguide to the Amphibians and Reptiles of Madagascar, 2nd edition. Köln, Germany: Privately Published. 480 pp.
- GRANDIDIER, A. 1893. Les voyageurs français à Madagascar pendant les trente dernières années. Bulletin de la Société de Géographie de Paris, ser. 7, **14**: 289-300.
- GREENE, H. W. 1988. Antipredator mechanisms in reptiles, pp. 1-152. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*, Vol. 16, Ecology B: Defense and Life History. New York: Alan R. Liss.
- GUIBÉ, J. 1954. Etude de *Liopholidophis lateralis* (D. et B.) et description d'une espèce nouvelle [Reptiles]. Mémoires de l'Institut Scientifique de Madagascar, ser. A, **9**: 241-246.
- . 1958. Les serpents de Madagascar. Mémoires de l'Institut Scientifique de Madagascar, ser. A, **12**: 189-260.
- GÜNTHER, A. 1872. Seventh account of new species of snakes in the collection of the British Museum. Annals and Magazine of Natural History, 9, ser. **4**(49): 13-37.
- . 1882. Ninth contribution to the knowledge of the fauna of Madagascar. Annals and Magazine of Natural History, **9**: 262-266.
- . 1890. Tenth contribution to the knowledge of the fauna of Madagascar. Annals and Magazine of Natural History, 5, ser. **6**: 69-72.
- GUYER, C., AND M. A. DONNELLY. 1990. Length-mass relationships among an assemblage of tropical snakes in Costa Rica. Journal of Tropical Ecology, **6**: 65-76.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1985. International Code of Zoological Nomenclature, 3rd edition. London: International Trust for Zoological Nomenclature. xx + 338 pp.
- JAN, G. "1863" [1862]. Enumerazione sistematica degli ofidi appartenenti al gruppo Coronellidae. Archivio per la Zoologia l'anatomia e la Fisiologia, **2**: 213-330.
- JAN, G., AND F. SORDELLI. 1879. *Iconographie Générale des Ophidiens*, Vol. 5, livr. 49, pl. II. Milan.
- JOURDRAN, E. "1904" [1903]. Les Ophidiens de Madagascar. Paris: A. Michalon. 63 pp. + 30 pls.
- KAUDERN, W. 1922. Sauropsiden aus Madagaskar. Zoologische Jahrbucher Abteilung für Systematik, **45**: 395-458.
- KLAUBER, L. M. 1943. Tail-length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. Bulletin of the Zoological Society of San Diego, **18**: 1-60.
- . 1945. Herpetological correlations. I. Correlations in homogeneous populations. Bulletin of the Zoological Society of San Diego, **21**: 1-101.
- LIDDELL, H. G., AND R. SCOTT. 1968. *A Greek-English Lexicon*. Oxford: Clarendon Press.
- MACPHEE, R. D. E. 1987. The shrew tenrecs of Madagascar: systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). American Museum Novitates, **2889**: 1-45.
- MAJOR, C. I. F. 1896. On the general results of a

- zoological expedition to Madagascar in 1894-96. Proceedings of the Zoological Society of London, **1896**: 971-981.
- MARX, H. 1958. Catalogue of type specimens of reptiles and amphibians in Chicago Natural History Museum. Fieldiana, Zoology, **36**(4): 409-496.
- MERTENS, R. 1933. Die Reptilien der Madagaskar-Expedition Prof. Dr. H. Bluntschili's. Senckenbergiana Biologica, **15**(3/4): 260-274.
- MOCQUARD, F. 1895a. Sur les reptiles recueillis à Madagascar de 1867 à 1885 par M. Grandidier. Bulletin de la Société Philomathique de Paris, ser. 8, **7**: 93-111.
- . 1895b. Sur une collection de reptiles recueillis à Madagascar par MM. Alluaud et Belly. Bulletin de la Société Philomathique de Paris, ser. 8, **7**: 112-135.
- . 1904. Description de quelques reptiles et d'un batracien nouveaux de la collection du Muséum. Bulletin du Muséum National d'Histoire Naturelle, Paris, **10**: 301-309.
- . 1908. Description de quelques reptiles et d'un batracien nouveaux de la collection du Muséum. Bulletin du Muséum National d'Histoire Naturelle, Paris, **14**: 259-262.
- . 1909. Synopsis des familles, genres et espèces des Reptiles écailleux et des Batraciens de Madagascar. Nouvelles Archives du Muséum, Paris, 5 ser., **I**: 1-110.
- MORGAN, E. C. 1973. Snakes of the subfamily Sibynophiinae. Ph.D. dissertation, University of Southwestern Louisiana, Lafayette. xiv + 260 pp.
- MYERS, C. W. 1973. A new genus for Andean snakes related to *Lygophis boursieri* and a new species. American Museum Novitates, **2522**: 1-37.
- . 1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bulletin of the American Museum of Natural History, **153**(1): 1-262.
- . 1986. An enigmatic new snake from the Peruvian Andes, with notes on the Xenodontini (Colubridae: Xenodontinae). American Museum Novitates, **2853**: 1-12.
- MYERS, C. W., AND J. E. CADLE. 1994. A new genus for South American snakes related to *Rhadinaea obtusa* Cope (Colubridae) and resurrection of *Taeniophallus* Cope for the "*Rhadinaea*" *brevivirostris* group. American Museum Novitates, **3102**: 1-33.
- MYERS, C. W., AND J. A. CAMPBELL. 1981. A new genus and species of colubrid snake from the Sierra Madre del Sur of Guerrero, Mexico. American Museum Novitates, **2708**: 1-20.
- NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. Gland, Switzerland: World Wildlife Fund. xvii + 374 pp.
- NOBILI, G. 1905. Descrizione di un nuovo potamonide di Madagascar. Bollettino dei Musei di Zoologia ed Anatomia Comparata della Università di Torino, **20**(507): 1-4.
- PARKER, H. W. 1925. New and rare reptiles and batrachians from Madagascar. Annals and Magazine of Natural History, ser. 9, **16**: 390-394.
- PERACCA, M. G. 1892. Descrizione di nuove specie di Rettili e Anfibi di Madagascar. Bollettino dei Musei di Zoologia ed Anatomia Comparata della Università di Torino, **7**(112): 1-5.
- . 1893. Descrizione di nuove specie di Rettili e Anfibi di Madagascar. Bollettino dei Musei di Zoologia ed Anatomia Comparata della Università di Torino, **8**(156): 1-16.
- PESANTES, O. S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology, **28**(1): 93-95.
- RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1994a. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. Biological Conservation, **69**: 65-73.
- . 1994b. A review of the Madagascan snake genera *Pseudoxyrhopus*, *Pararhadinaea*, and *Heteroliodon* (Squamata: Colubridae). Miscellaneous Publications of the Museum of Zoology, University of Michigan, **182**: 1-37.
- SAVITZKY, A. H. 1981. Hinged teeth in snakes: an adaptation for swallowing hard-bodied prey. Science, **212**: 346-349.
- . 1983. Coadapted character complexes among snakes: fossoriality, piscivory, and durophagy. American Zoologist, **23**: 397-409.
- SHINE, R. 1983. Reptilian reproductive modes: the oviparity-viviparity continuum. Herpetologica, **39**: 1-8.
- . 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. American Naturalist, **138**(1): 103-122.
- UICN/PNUE/WWF (UNION INTERNATIONALE POUR LA CONSERVATION DE LA NATURE/PROGRAMME DES NATIONS UNIES POUR L'ENVIRONNEMENT/WORLD WILDLIFE FUND). 1990. Madagascar: Profil de l'environnement. Gland, Switzerland, and Cambridge, England: UICN. xv + 439 pp.
- WERNER, F. 1929. Übersicht der Gattungen und Arten der Schlangen der Familie Colubridae III. Teil (Colubrinae). Mit einem Nachtrag zu den übrigen Familien. Zoologische Jahrbücher Abteilung für Systematik, **57**: 1-196.
- WILLIAMS, K. L., AND V. WALLACH. 1989. Snakes of the World, Vol. 1, Synopsis of Snake Generic Names. Malabar, Florida: Krieger Publishing. viii + 234 pp.
- ZEHR, D. R. 1962. Stages in the normal development of the common garter snake, *Thamnophis sirtalis sirtalis*. Copeia, **1962**: 322-329.